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Examining neotropical primate community structure at regional and local scales : insights from taxonomic and phylogenetic approaches

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EXAMINING NEOTROPICAL PRIMATE COMMUNITY STRUCTURE AT REGIONAL AND LOCAL SCALES: INSIGHTS FROM TAXONOMIC AND PHYLOGENETIC APPROACHES

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To my family

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ABSTRACT

Understanding mechanisms underlying the distribution of biodiversity remains a central issue in ecology. In my dissertation I integrate ecological and phylogenetic information at multiple spatial scales to better understand neotropical primate distribution and community structure. Initially, I investigate the variation within species ranges in relation to species richness and patterns of species relatedness. Results suggest a positive association among primate species throughout their distributions, whereby species tend to present higher richness within their ranges than average richness for the entire taxon. However, comparing empirical distributions to a null model of range cohesion, this positive association is lower than expected. This suggests mechanisms other than dispersal are setting a limit to the number of species that can co-occur throughout a species' range. These differences in species associations across geographic ranges generate variation in local community composition. I analyzed the relative contribution of ecological, historical and spatial processes in determining taxonomic and phylogenetic community structure across 74 sites throughout the Neotropics. Spatial predictors explained most of the independent variation for taxonomic and phylogenetic metrics, suggesting spatial processes, such as dispersal limitation, are important for determining community structure. Most of the contribution of ecological (environmental) predictors was associated with spatial processes, evincing the importance of environmental and spatial gradients in determining change in community structure. While the overall contributions of these predictors were similar for taxonomic and phylogenetic metrics, analyses of phylogenetic metrics independently evidenced more complex relationships. At local communities, niche differentiation is expected to allow species coexistence. However, these differences may reflect evolutionary constraints of species, rather than active selection. I investigate niche overlap and presence of niche conservatism for primate species at three communities. For the niche characteristics measured by my study, I find no significant differences in niches of closely related species within sites. However, when comparing niches across sites, significant differences arise between populations of the same species or closely related species. These findings suggest ecological differentiation may be acting at large spatial scales promoting niche differentiation, while at local scales phylogenetic constraints may be a stronger driver of community structure. Results of this dissertation generate valuable insights regarding our understanding of mechanisms responsible for generating and maintaining community structure for a highly diverse tropical mammal radiation.

CHAPTER 1. INTRODUCTION

Species coexist. This statement, in its simplicity, is a remarkably accurate description of the natural world (Tokeshi, 1999). This coexistence generates a diversity of multispecies assemblages (*i.e.* communities) with intrinsic characteristics. While spatial variation in species composition is one of the most fundamental and conspicuous features in nature, species coexistence is a major issue in community ecology. It underlies multiple aspects of community organization, from local-scale within assemblage patterns to large-scale geographical patterns. In this dissertation I address the issue of species coexistence and community structure of neotropical primates by integrating ecological and evolutionary processes at multiple spatial scales.

Coexistence, community structure and the multifaceted nature of biodiversity

Understanding mechanisms responsible for generation and maintenance of community structure remains a central question in ecology. From a deterministic perspective, community structure is expected to be driven by niche differentiation according to the competitive exclusion principle (Gause, 1934). Thus, deterministic models describe local communities as non-random sets of species, sorted according to physiologically and ecologically defined niches (Hutchinson, 1957). In contrast, stochastic perspectives, one of which is the recently developed neutral model (Hubbell, 2001), ignore species-specific traits, and emphasize the importance of colonization-extinction dynamics as a key driver of community assembly. Lastly, biogeographical and macro-evolutionary processes, such as speciation, colonization and historical dispersal events, have also been shown to alter community structure by influencing the regional species pool from which communities are assembled (Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004). Recently, there has been an increasing interest in investigating simultaneously the effects of multiple mechanisms of assembly, and to examine importance and magnitude of their relative effects (Leibold & McPeek, 2006; Qian, 2008).

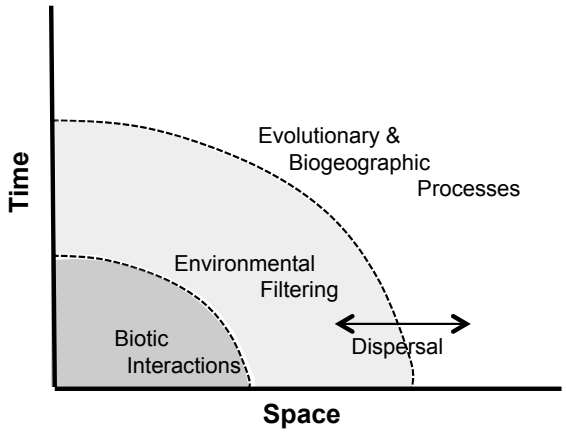

Figure 1.1. Schematic of the interplay of mechanisms driving species distribution and community assembly at multiple spatial and temporal scales. Modified from Cavender-Bares *et al*. (2009).

Local and regional perspectives are now organized along a continuum, from niche-assembly to dispersal assembly theory (Chase & Myers, 2011), with the relative influence of these processes changing with varying temporal scales and depending fundamentally on the spatial scale of analysis (Figure 1.1).

At the largest spatial and temporal scales, differences in species distributions are determined principally by biogeographical processes (*i.e*. speciation, extinction and dispersal). Influence of dispersal is dependent on the vagility of an organism and can influence patterns of species distribution established through ecological sorting processes (Vamosi *et al*., 2009). At intermediate spatial scales, environmental filtering removes species lacking physiological tolerances that allow their persistence under given environmental conditions (temperature, soil moisture, light availability, pH). Biotic interactions are thought to be more intense at local scales. These processes, such as competition, disease, herbivory, facilitation and mutualism may interact with the abiotic environment to reinforce or diminish habitat filtering. Methods that allow partitioning of variance among causal factors driving community assembly facilitate better understanding of these mechanisms.

Variation in species distribution and community composition is not only evident at the taxonomic level (numbers of species), but is expressed across the entire "phenotype" of biodiversity. Different measures of biological diversity have been proposed (see Izsak & Papp, 2000; Magurran & McGill, 2011) including those focused on taxonomic diversity (taxonomic identity of species), functional diversity (the functional role species are playing in an ecosystem) and phylogenetic diversity (amount of evolutionary history each species contributes). Taxonomic diversity, particularly species richness (McIntosh, 1967) is by far the most commonly used measure, since species are the fundamental units of ecological research. However, it does not take into account dissimilarities among species in terms of their ecological functions or evolutionary histories, and thus cannot alone describe processes involved in species coexistence and ecosystem functioning (Cianciaruso, 2011). Measures of phylogenetic diversity account for evolutionary history shared among species (Faith, 1992; Webb, 2000). Although community phylogenetics is a relatively new area of research (Webb *et al*., 2002), it has provided valuable insights regarding the roles of species interactions and biogeographic histories in assembly of communities from a regional pool (see Cavender-Bares *et al*., 2009; Vamosi *et al*., 2009 for extensive reviews).

Studies of phylogenetic community structure have been undertaken for many taxa, ranging from microbes to plants, insects, birds, and mammals. Based on a conceptual framework provided by Webb *et al*. (2002), linking phylogenetic niche conservatism (the tendency of species to retain ancestral ecological characteristics; Wiens & Graham, 2005) with different assembly processes allows predictions regarding patterns of phylogenetic relatedness. For instance, patterns of phylogenetic clustering are commonly interpreted as evidence for environmental filtering of phylogenetically conserved traits (Webb, 2000; Horner-Devine & Bohannan, 2006; Vamosi & Vamosi, 2007). On the other hand, phylogenetic evenness is

considered evidence either for limiting similarity due to competition between closely related species when niches are phylogenetically conserved (Lovette & Hochachka, 2006) or environmental filtering of traits that evolved convergently (Cavender-Bares *et al*., 2004; Helmus *et al*., 2007). Furthermore, correlating species diversity with phylogenetic diversity has also allowed the elucidation of the sequence of speciation and dispersal events in the process of community assembly, as Cardillo *et al*. (2008) show for island mammal assemblages. Here patterns of low phylogenetic divergence within an island, despite high local richness indicated that oceanic islands were predominantly shaped by colonization and endemic speciation. Combining information regarding the phylogenetic diversity of an area with its species richness allows also for inferences regarding hotspots of recent adaptive radiation that were formed by sympatric species that subsequently diversified extensively (*e.g*. sedges in the Cape floristic region of South Africa, Slingsby & Verboom, 2006).

The substantial increase of studies in phylogenetic community ecology in the past decade (Cianciaruso, 2011) has provided ample evidence for the validity of these methods to provide a link between evolutionary and biogeographic history and present-day ecology. Nonetheless, it is important to consider that processes of community assembly (ecological or evolutionary) may lead to different patterns depending on the spatio-temporal scale of investigation. Identifying pertinent scales of variation in mechanisms responsible for generating and maintaining community structure requires integrating different types of information. Macroecology attempts to combine these views and reach a consensus understanding of how processes such as speciation, dispersal and niche dynamics shape large-scale species patterns of diversity (Brown, 1995). Data on species responses to environmental variation and species-habitat relationships is coupled with information on influence of regional and historical processes, which potentially limit number and identity of species in the regional pool from which local communities are assembled (Ricklefs, 1987). Traditional ideas regarding community structure invoked local resource competition and niche diversification as central determinants of species membership at local scales (Diamond, 1975; Strong *et al*., 1984). On the other hand, historical changes in regional climates, evolutionary and large-scale biogeographic processes, such as dispersal and colonization are fundamental in shaping local communities (Ricklefs & Schluter, 1993; Leibold *et al*., 2004; Graham & Fine, 2008). Combining information on multiple aspects of diversity, and comparing processes among different spatial scales should provide a better understanding of the mechanisms responsible for species distribution and community structure.

Study group

Neotropical primates are the result of a single colonization event during the early Oligocene and have since diversified over a relatively short period of time (Schrago, 2007). The earliest fossil (*Branisella boliviana*) dates back to the late Oligocene of Bolivia, approximately 26 my. As several modern lineages have been traced to ancestral forms that inhabited forested regions of Amazonia 12–16 my, it has been argued that the radiation of extant platyrrhines is principally Amazonian in origin (Hartwig & Meldrum, 2002). However, recent studies identify four

different regions in South America (Amazonian, Atlantic, Patagonian and Caribbean) where individual primate taxa appear to have diversified in response to differing habitat configurations (Rosenberger *et al*., 2009). This complex history of diversification has led to a widely ranging group, representing many different events of radiation and colonization. Currently, platyrrhines are distributed from southern Mexico to northern Argentina, living in a wide variety of habitats: dry coastal forest, montane forest, gallery forests, *terra-firme* and seasonally flooded tropical rainforest (Emmons & Feer, 1997).

Platyrrhines comprise a group of four families, fifteen genera and over 120 species (Groves, 2005). The Neotropics present some of the most species rich communities within the entire Primate order, with up to 14 species living in sympatry (Peres, 1993). In addition to their taxonomic diversity, neotropical primates present remarkable variation in terms of their morphology, behavior and habitat use (see Kinzey, 1997). This group varies widely in adult body size, with the smallest species, the pygmy marmoset (*Cebuella pygmaea*), weighing 120 g and the largest species, the muriqui (*Brachyteles arachnoides*) and the gray woolly monkey (*Lagothrix cana*) weighing 10–12 kg (Nowak, 1999). The platyrrhine radiation is characterized by a number of different foraging strategies, patterns of habitat utilization, and anatomical adaptations that enable species to efficiently exploit food types such as insects, small vertebrates, immature and mature leaves, hard unripe fruits and soft ripe fruits, nuts, seeds, exudates, fungi, and floral nectar (Norconk *et al*., 2008).

Neotropical primates are a good group for studying relative influences of ecological, evolutionary and neutral mechanisms of community assembly at both regional and local scales. Their morphological and behavioral variability is thought to reflect influence of biotic and ecological processes at local scales, resulting in communities where competition is reduced through spatial and temporal partitioning of niche space (Terborgh, 1983; Peres, 1993), and resource use (Stevenson *et al*., 2000). Additionally, local environmental variation, particularly seasonality, may have an ecological (abiotic) effect, as it alters resource availability and soil nutrient composition, which in turn influences plant nutrient quality (Janson & Chapman, 1999). Primates, in particular small insectivores, are directly influenced by seasonal floods, as these severely disrupt availability of understory arthropods and prey foraging substrates (Peres, 1997). On the other hand, evolutionary and historical processes may also have an effect on local community composition. Large scale distribution of primate species is tightly linked to forested areas they inhabit (Haffer, 1997) and riverine barriers which act as dispersal barriers, promoting allopatric speciation (Ayres & Clutton-Brock, 1992). At a regional scale, it has been determined that both environmental factors (Reed & Fleagle, 1995; Kay *et al*., 1997) and historical events (Lawes & Eeley, 2000) influence patterns of regional-scale variation in primate species richness. However, few studies have addressed their influence on community composition (Peres & Janson, 1999; Kamilar, 2009; Beaudrot & Marshall, 2011). Currently only one study has attempted to evaluate hypotheses in other components of biodiversity, finding low levels of phylogenetic structure in neotropical assemblages (Kamilar & Guidi, 2010). Further investigation of these communities combining information on multiple aspects of diversity at

different spatial scales will provide valuable insights regarding tropical diversity.

Overview of chapters

In this dissertation, I take an integrative approach to better understand mechanisms responsible for local and regional-scale patterns of species co-occurrence and structure of neotropical primate communities. I address this goal from ecological and evolutionary perspectives in an attempt to link short term-local processes to regional-historical processes that occur at broader spatial and evolutionary scales.

Many ecological phenomenon, such as species-area relationships, spatial turnover and the geographic variation in species richness, are inherently determined by the size, spatial location and numerical distribution of species' ranges (Gaston, 1991). While determinants of geographical range sizes have been thoroughly studied (Brown *et al.,* 1996), there is still much information that can be inferred from these basic tools (Baselga *et al*., 2012). In chapter 2, I apply recently developed methods to analyze the internal structure of species ranges. Diversity characterize spatial variation in species richness and composition across sites within the distribution of a given species (Arita *et al*., 2008). Similarly, phylogenetic fields describe the patterns of relatedness among species ovelaying a focal species' geographic distribution (Villalobos *et al*., 2013). I use presence/absence matrix based on the distributions of 108 primate species using range maps from NatureServe (Patterson *et al*., 2007) to characterize how diversity and phylogenetic attributes of co-occurring species vary in relation to species richness throughout the ranges of individual species. While the properties of species diversity fields are determined in part by the sizes, shapes and locations of geographic ranges (Villalobos & Arita, 2010), findings suggest there is phylogenetic signal in some of these attributes. Neotropical primate species diversity and phylogenetic fields showed high levels of co-occurrence across the Amazon basin, with a decrease towards higher latitudes. Findings from these analyses allow the investigation of mechanisms of species co-occurrence at macroecological and biogeographic scales.

In chapter 3, I evaluate the relative importance of niche, historical and spatial processes on the taxonomic and phylogenetic structure of primate communities across the Neotropics. Data on community composition for 74 sites were gathered from the literature, and communities were characterized based on taxonomic and phylogenetic composition. Three predictive matrices were used as explanatory variables representing ecological (environmental), historical (riverine barriers and Pleistocene refugia) and dispersal-based spatial hypotheses (vectors of spatial principal coordinates of neighboring matrices based on geographic coordinates). Here I conducted variation partitioning analyses to decouple independent and shared effects of these predictors. I found that purely spatial processes, such as dispersal limitation, play a stronger role in structuring primate communities than niche mechanisms and historical events. These results are in concordance with studies of primate communities in the neotropics (Kamilar, 2009; Beaudrot & Marshall, 2011). The influence of ecological and evolutionary mechanisms

structuring primate communities was conflated with spatial processes, which suggests that community structure is determined by spatial mechanisms reflecting environmental gradients and biogeographic processes. Although the relative contribution of each predictor variable was similar between different aspects of diversity, examining phylogenetic metrics independently, it was evidenced that ecological, historical and spatial mechanisms interact in complex ways to determine current patterns of phylogenetic community structure.

Moving from a regional to a local scale, in chapter 4 I determine whether primate habitat preferences at three sites in Ecuador are the result of species ecological flexibility to habitat availability, or whether species habitat and resource use is constrained by evolutionary history (*i.e*. do primate species show evidence of phylogenetic niche conservatism?). I assessed the structural axis of species' ecological niches at each site, and determined whether there was evidence of niche conservatism at this local scale. Ten primate species were surveyed in these communities, and their habitat preferences were recorded using standardized habitat assessment plots at each site. Results indicate that primate species show preferences for particular habitat features. Within sites, closely related species tend to have niches that are not significantly different, while species from different families show significant niche differences. In contrast, niches of closely related species across sites are significantly different. There was not a significant relationship between ecological and phylogenetic distance when investigating species across sites, indicating a minimal extent of niche conservatism on ecological niche axes measured in this study. Here I advocate these differences can be related to changes in strength of inter/intraspecific competition and resource availability across sites. Characterizing multiple axes of the ecological niche can provide important insights when investigating mechanisms responsible for maintenance of community structure.

In the last chapter, I summarize results from chapters 2-4 considering their implications regarding neotropical primate distribution and community structure. Different chapters of this dissertation tie together the disciplines of macroecology and community ecology by incorporating phylogenetic information to understand processes responsible for the structure of communities of this highly diverse tropical taxon.

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CHAPTER 2. LARGE SCALE PATTERNS OF CO-OCCURRENCE OF NEOTROPICAL PRIMATES: EXAMINING THE INTERNAL STRUCTURE OF SPECIES RANGES

Introduction

Understanding large-scale patterns of distribution of species richness remains one of the major goals in biogeography and macroecology (Rosenzweig, 1995). Geographic variation in species richness is the result of the overlap of species ranges. However, this overlap may arise because of multiple mechanisms, such as similar ecological requirements of species (Webb, 2000; Currie *et al*., 2004), dispersal limitation (Hubbell, 2001; Svenning *et al*., 2011) or constraints given by the shape and extent of the geographical domain (*i.e*. mid-domain effect, Colwell & Hurtt, 1994; Jetz & Rahbek, 2001; Tello & Stevens, 2012). While species interactions are known to affect species co-occurrence at local scales (Gotelli & McCabe, 2002), the importance of species associations and differential co-occurrence in determining species distribution at regional scales will provide insight regarding mechanisms determining the assembly and maintenance of biodiversity (Gotelli *et al*., 1997; Borregaard *et al*., 2010).

The most common tools for large-scale analyses of diversity are range maps that depict the distribution of species across a given domain (Brown, 1995). Overlaying species ranges onto quadrats of equal size can be used to represent spatial variation in species richness on continental and global scales. Richness patterns can be summarized in a species' by site presence-absence matrix (PAM), where rows represent taxa, columns correspond to localities (or cells in a grid), and the contents of a cell corresponds to presence (1) or absence (0) of a given species at a given site (Gotelli, 2000). PAMs combine information on species richness of sites (column sums), range sizes of species (row sums), and co-occurrence across space (measured by the degree of covariance in the matrix). These matrices summarize two fundamental units of biogeography: the distributional range of species (Brown *et al*., 1996; Gaston, 2003) and species diversity (the number of species occurring in a given site; Rosenzweig, 1995). PAMs have traditionally been analyzed by rows (*R*-mode) or by columns (*Q*-mode). The sum along a column (*Q*-mode) is the species richness of a site (Fig 2.1a). This variable has been widely used to test multiple hypotheses regarding determinants of variation in distribution of biodiversity (Hawkins *et al*., 2003; Willig *et al*., 2003) and for identifying hotspots of diversity (Ceballos *et al*., 2005; Mouillot & Gaston, 2009). Conversely, the sum of elements along a row (*R*-mode) represents the occupancy of a species, that is, the range size of a species across a given domain (Fig 2.1b). Information generated from this approach has primarily been used to assess whether general assembly rules (Diamond, 1975) determine composition of local communities. Lastly, the fill of PAMs has been an important tool for analyzing species co-occurrence, with the aid of null models (Gotelli, 2000; Gotelli & McCabe, 2002), that randomize the elements of the PAM but conserve row and/or column totals (Gotelli, 2000).

While these approaches have provided much information regarding species diversity, distribution and co-occurrence, there still remains much information to be inferred from PAMs.

Particularly, simultaneously measuring distribution and diversity in analyses by species (*RQ*-mode) or by sites (*QR*-mode) allows investigating constraints in the fill of the matrix by considering interactions between rows and columns. In *RQ*-mode, analyses of species ranges (n_i) are enhanced by incorporating values of species richness (s_j) of sites in which a focal species occurs to generate 'diversity fields' (Fig 2.1c). Diversity fields characterize spatial variation in species richness and composition across sites within the distribution of a particular species (Arita *et al*., 2008).

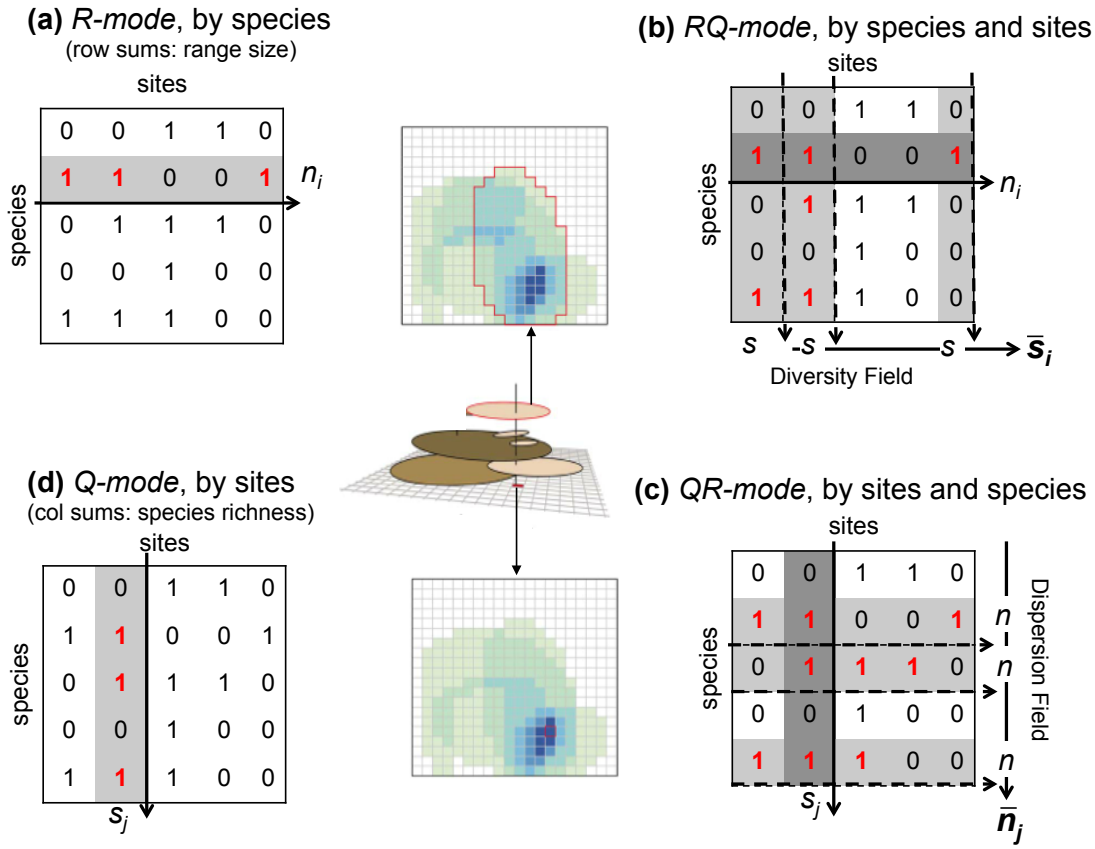

Figure 2.1: Diversity and distribution in presence-absence matrices. In traditional analyses (*a*, *b*), the range size of species (n_i) or the species richness of sites (s_j) are computed by summing elements along rows (*R*-mode) or columns (*Q*-mode), respectively. In the *RQ*-mode (c), analyses by species (row sums) are enhanced by incorporating information regarding the species richness (column totals) of sites in which a focal species occurs to generate 'diversity fields'. Then, mean richness of those sites where species *i* occurs can be calculated ($\bar{s}_i$). In *QR*-mode (d) sites analyses are enriched by considering the range size distribution (row totals) of species occurring in a focal site to generate 'dispersion fields'. Mean range size of those species occurring at site *j* can then be calculated ($\bar{n}_j$). The central panel illustrates dispersion fields and diversity fields of Graves and Rahbek (2005) and Arita *et al*. (2008), respectively. The center diagram represents a schematic illustration of elliptical ranges. Vertical line indicates a focal cell (marked as a red square) for the dispersion fields shown in the bottom panel. A red ellipse illustrates a focal range for the diversity field displayed in the top panel (Modified from Arita *et al*., 2008; Borreghard & Rahbek, 2010).

Conversely, in *QR*-mode analyses, data are computed by columns (s_j), but consider the structure of the rows (n_i) that intersect a given column (*i.e.* range size of species occurring in the focal site), to generate the "dispersion field" of a site. Dispersion fields represent the distribution of geographical range sizes of all species that occur at a given site (Graves & Rahbek, 2005).

Aspects such as size, shape and location of individual ranges (Brown *et al*. 1996) are important features determining some of the most common large-scale patterns of diversity such as latitudinal gradients (Willig *et al*., 2003), species-area and species-abundance relationships (Connor & McCoy, 2001). Examination of how species richness changes within the distribution of individual species' ranges (*i.e.* internal structure), as proposed in the 'diversity field' approach can provide great insights into our understanding of these patterns (Arita & Rodriguez, 2002). Thus far diversity fields have investigated the internal structure of ranges in terms of geographic variation in the number of overlaps with other species (*i.e.* patterns of variation of species richness among grid cells composing a species geographic range), and explained it in terms of the tendency of species to occur in species-rich or species-poor locations (Villalobos & Arita, 2010; Soberón & Ceballos, 2011). Recently Villalobos and Arita (2010) produced diversity fields to characterize variation in richness of co-occurring species within the distribution of bat species in the New World. Their findings suggest that mean species richness of sites within the range of a taxon is related to its range size. Furthermore, these results indicate that even within species with relatively small ranges, that share similar feeding habits, the internal structure of their ranges is highly variable.

As biodiversity is a multifaceted phenomenon, investigating the internal structure of species ranges from phylogenetic and functional perspectives may also provide valuable insights regarding large-scale patterns of diversity and species co-occurrence. For instance, Villalobos *et al*. (2013a) proposed species phylogenetic fields as a way to characterize the overall phylogenetic structure contained within a range including the focal species. Phylogenetic fields investigate the average degree of relatedness of species within focal species' ranges. Exploration of how species relatedness varies across individual ranges may allow consideration of the role of speciation, local dispersal limitation and biogeography in determining patterns of species association and their distribution across a domain. At large spatial scales, phylogenetic patterns by sites can be strongly influenced by the biogeography of speciation and how it interacts with movement or stability of geographical ranges (Vamosi & Vamosi, 2009). For instance, close relatives may be unlikely to co-occur if speciation is mostly allopatric and geographical ranges are relatively stable through time (Johnson & Stinchcombe 2007); while frequent sympatric speciation (or more commonly) with similarly stable range boundaries could drive a pattern of phylogenetic clustering.

Here I conducted an analysis of diversity and phylogenetic fields for primate species across the Neotropics. Neotropical primates are an ideal group for macroecological analyses, as they represent one of the most taxonomically, behaviorally, and anatomically diverse primate radiations, distributed across the largest extent of tropical forest in the world (Garber *et al*.,

2008). Geographic patterns of neotropical primate biodiversity are thought to be the result of processes related to dispersal limitation (Beaudrot & Marshall, 2011; Gavilanez & Stevens, 2012), historical (Kamilar, 2009) and biogeographic events (Ayres & Clutton-Brock, 1992), coupled with high tropical productivity (Kay *et al.,* 1997), that create some of the most species rich primate assemblages. Furthermore, the availability of a well-resolved phylogeny for this taxon (Fabre *et al*., 2009) allows incorporating information regarding species evolutionary relatedness into analyses of the internal structure of species ranges. I examined how the internal structure of species ranges changes in relation to diversity and phylogenetic parameters, and explored possible ecological and evolutionary mechanisms driving these patterns. These analyses provide a link between macroecological inferences and evolutionary history to better understand large-scale patterns of biodiversity.

Methods

Data on the continental distributions of 108 neotropical primate species were obtained from the Nature Serve database (Patterson *et al*., 2007). A grid of 5087 equal-area cells (2500 km^2, corresponding to approximately an area of 0.5° x 0.5° latitude and longitude near the Equator) was overlaid on the distribution maps of 108 primate species to generate a presence/absence matrix (PAM) of 5087 columns and 108 rows. The sum of elements along rows of the matrix returned the range sizes of species (n_i), measured as the number of quadrats that are overlapped by the range map of each species. The number of range maps that overlapped a given site represented the species richness of that site (s_j) that equals the sum of elements of the column of the PAM corresponding to that site. Following Arita *et al*. (2008) all richness and range size variables were converted to proportional values by dividing them by the corresponding total of species (S_{108}) or quadrats for the whole system (N_{5087}). Richness values divided by S represented the proportional species richness of site j (s_j*), and any range size value divided by N corresponded to the proportional range size of species i (n_i*).

Diversity Fields – Diversity fields for each species were calculated based on the set of species-richness values of quadrats in which the focal species occurs, following an RQ mode of analysis of the PAM (Fig 2.1c). Diversity fields corresponded to vectors of length equal to the range size of species, representing variation in species richness across the cells in the range of a focal species (See Appendix A1 for a description of the procedure). Following Villalobos & Arita (2010) I described and examined statistical parameters and spatial variation of diversity fields of neotropical primate species. I used the standard statistical parameters of central tendency, deviation and shape (mean, variance and skewness) to examine species richness frequency distributions (SRFDs). Additionally, for each species, a histogram of its SRFDs was associated with a range map showing variation in internal structure of the range. These maps allowed visualization of structure of ranges as spatial patterns of co-occurrence, and relatedness, with other species.

Range–diversity plots allow the simultaneous representation of diversity and distributional data generated by diversity fields (Arita *et al*., 2008). Data to generate these plots is obtained from the PAM (see Figure 2.2), combining information from columns and rows. Ordinates are proportional range sizes (n_i*) and abscissas are average species richness within their ranges (s_i*). Histograms on top and on the right-hand side of Fig. 2.2 show frequency distributions of those variables. Dark curved lines in Fig. 2.2 represent mathematical constraints that set a limit to the possible values of points (species) in the range diversity plot. Shape and position depends on quantitative characteristics of the PAM such as, minimum and maximum richness and range size values (Arita *et al*., 2008; 2012). The dispersion of points within those limits depends on the overall covariance among species that is ultimately determined by the patterns of species' co-occurrence. A species covariance with respect to others depends on the number of species with which it shares its distribution (Arita *et al*., 2008). The vertical dashed line corresponds to the mean proportional species richness of sites ($\bar{s}$*= *f**).

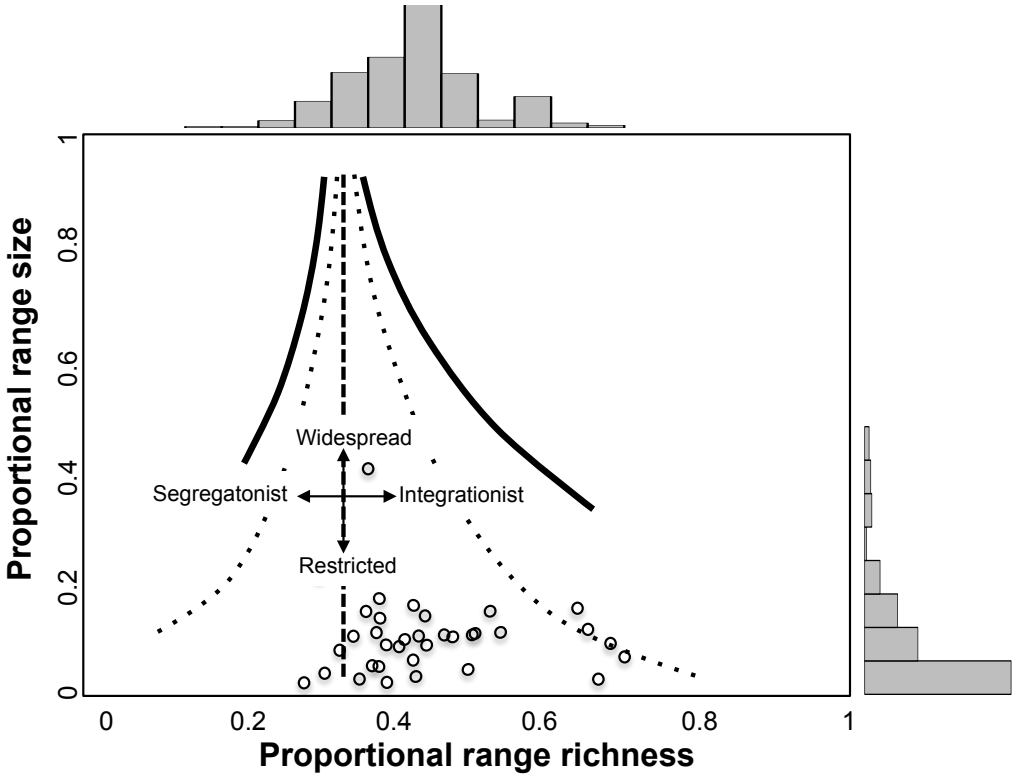

Figure 2.2. Schematic representation of range-diversity plots by species. Solid thick curved lines mark the upper theoretical limit for species (open circles). Vertical dashed line corresponds to the mean proportional range richness (proportional fill of the PAM f^*). The hyperbolic dotted curves are lines of equal covariance among species. Histograms on top and on the right-hand side represent frequency distributions of proportional range richness and proportional range size across all cells, respectively. Modified form Villalobos *et al*. (2013b)

The thin dotted hyperbolic lines in Fig. 2.2 correspond to lines of equal covariance among species, used as references to determine the level of association among species. Right-side line represents positive covariances, and left-side line corresponds to negative covariances. Points arranging to the right side of this line correspond to species with higher covariance than the average range richness for the entire region (*i.e.* species that co-occur with more species than the regional mean, integrationists), while points to the left of this line represent species that co-occur with fewer species than the average regional mean (segregationists). Range-diversity plots and its associated parameters were obtained using the script available from Arita *et al*. (2012) in the statistical language R (R development Core Team, 2013)

Phylogenetic fields – I used a primate phylogeny obtained from Fabre *et al*. (2009) to analyze species phylogenetic fields. Here I used mean pairwise distance (MPD; Webb, 2000) and mean nearest taxon distance (MNTD; Webb, 2000) to characterize the phylogenetic structure present within the geographic range of focal species. These metrics describe different components of phylogenetic diversity. MPD takes into account all pair-wise distances among all species in a cell, providing an overall measure of phylogenetic diversity. MNTD quantifies distances between nearest-neighbors, and so, describes the degree that species in a cell within a range are terminally clustered (Webb, 2000). Phylogenetic fields were represented in two ways. First, following Villalobos *et al*. (2013a), I assessed the phylogenetic structure of a species' diversity field by determining the relatedness of species co-occurring within its range measured as the mean pairwise distance (MPD_{sp}; Webb, 2000) and mean nearest taxon distance ($MNTD_{sp}$; Webb, 2000) of species. In addition, I assessed the spatial change in phylogenetic relatedness of species across individual ranges by calculating MPD and MNTD of cells within the range of each species. Phylogenetic structure within individual species ranges was described by examining the standard statistical parameters of central tendency, deviation and shape of their phylogenetic frequency distributions (FDs), that is, the first (mean), second (variance) and third (skewness) moments, for each species. Additionally, histograms of mean MPD and MNTD FDs were associated with their corresponding range map, evidencing the variation in the internal structure of species ranges.

I used the Blomberg's *K*-statistic (Blomberg *et al*., 2003) to test for phylogenetic signal in attributes of species diversity and phylogenetic fields (range size, SR_{mean}, $SR_{var,}$ $SR_{skew,}$ MPD_{sp}, MPD_{mean}, MPD_{var}, MPD_{skew}, $MNTD_{sp}$, $MNTD_{mean}$, $MNTD_{var}$, $MNTD_{skew}$) using the R package Picante (Kembel *et al*., 2010). The *K* statistic compares observed signal in a trait to signal under a Brownian motion model of trait evolution on a phylogeny. *K* values of 1 correspond to a Brownian motion process that implies some degree of phylogenetic signal. *K* values closer to zero correspond to a random or convergent pattern of evolution, while *K* values greater than 1 indicate strong phylogenetic signal. To explore association between phylogenetic field (mean, variance and skewness of MPD and MNTD, MPD_{sp} and $MNTD_{sp}$) and diversity field attributes (SR_{mean}, $SR_{var,}$ SR_{skew}) and range size, I used phylogenetic generalized least squares (PGLS) regression analyses (Freckleton *et al*., 2002). These models account for shared evolutionary history of clades, and thus non-independence of data points, by incorporating an estimate of the

covariance of residuals resulting from shared ancestry in the error term (lambda, λ). The maximum likelihood estimate of λ corresponds to the transformation of the variance-covariance matrix of the linear model that best fits a Brownian motion model of evolution (Freckleton *et al*., 2002). λ ranges between 0 (no phylogenetic signal) and 1 (variation in the trait values is predicted by phylogeny; Pagel, 1997).

Null models – I used a spreading-dye algorithm of range cohesion (Jetz & Rahbek, 2001) to determine if observed patterns in taxonomic and phylogenetic diversity fields differed from those expected by chance. In this model, for each species, one cell from throughout the domain is selected and the species is assigned to this cell. Starting at this initial cell, "dispersers" are allowed to colonize only surrounding cells. This process is iterated until the number of cells occupied by the simulated range matches the empirical size for that species. The simulation continues to create geographic ranges following the same steps for all species in the clade. This model generates random, cohesive ranges with size equal to the empirical ranges, but with varied shape and spatial distribution across the domain. This null model assumes dispersal limitation in the production of species ranges, but constructs ranges irrespective of underlying environmental gradients. Furthermore, the location of any species is independent of the location of all others, removing historical effects, such as sister species diverging from a common ancestor. Randomized diversity and phylogenetic field parameters were calculated for each simulation and averaged for comparison with empirical values creating confidence intervals for simulated data. Phylogenetic analyses and null models were conducted and run in R (R Development Core Team, 2013) using packages Ape (Paradis *et al*., 2004) and Picante (Kembel *et al*., 2010).

Results

Throughout the distribution of neotropical primates, the number of ranges overlapping a given 50x50 km cell ranged from 1 to 20. Geographic ranges of species varied in size from 2 quadrats for highly restricted species (*e.g. Leontopithecus caissara*) to 2041 quadrats for *Cebus apella* (a species whose range covers 40% of the total extent of distribution of neotropical primates). Mean species richness for all cells was 5.56 (+/- 13.1) and mean range size of species was 629,400 km^2 (251.76 quadrats). Mean range-richness (average species richness within individual species ranges) was 8.28 (+/- 11.636). Cells with higher species richness were located in the Amazon basin near large rivers, and species richness declined towards northern and southern extremes (Fig. 2.3a). The phylogenetic structure of assemblages within each cell of the domain showed geographic structuring, particularly for MNTD. MPD was relatively high throughout the entire domain, with low values only in cells at higher latitudes (Fig. 2.3b). Assemblages located throughout the Amazon basin, at lower latitudes presented lower MNTD values than those at higher latitudes (Fig. 2.3c), while at the extremes of the distribution cells present high MNTD values.

Spatial variation in parameters of species diversity and phylogenetic fields – The frequency distributions of diversity and phylogenetic field parameters (mean, variance and skewness of SR,

MPD and MNTD) showed great variation (see Table A2 in Appendix A). Figure 2.4 presents some examples of these frequency distributions and spatial variation for species ranging in body size with different range sizes.

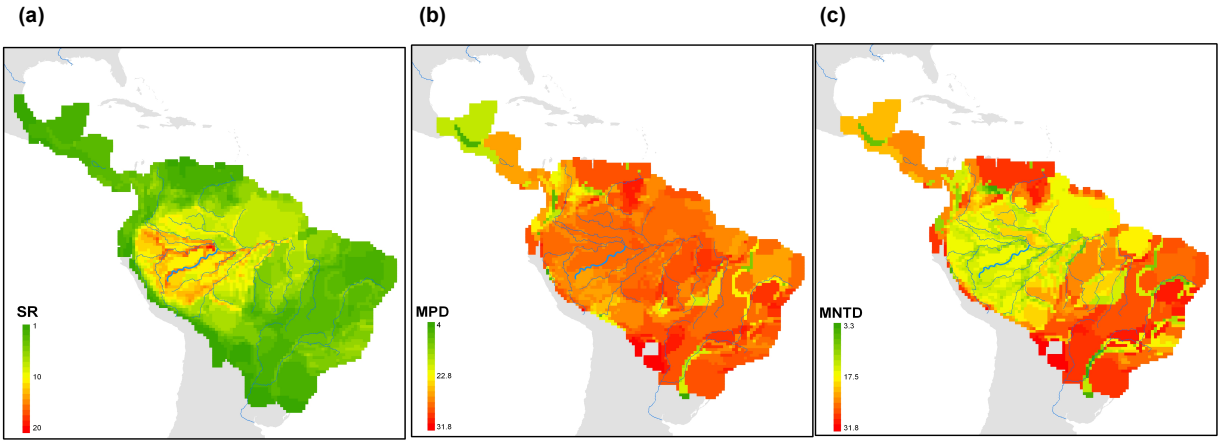

Figure 2.3. Geographic variation of (a) species richness, (b) Mean Pairwise Distance-MPD and (c) Mean Nearest Taxon Distance MNTD; for neotropical primate assemblages present at each 50x50 km cells of their distribution. Maps were created using Arc-GIS 9.3 (ESRI, 2008).

Callithix flaviceps, a small species endemic to south-eastern Brazil occurred in areas of intermediate species richness (SR_{mean} = 6.08; SR_{var} = 0.44; Fig. 2.4a). Mean pairwise distance was high, and homogeneous throughout its range (MPD_{mean} = 27.07, MPD_{var} = 0.44), and it co-occurred with more closely related species in the northernmost area of its range ($MNTD_{mean}$ = 18.59, $MNTD_{var}$ = 1.14). For all three frequency distributions (SR, MPD and MNTD) skewness was negative, indicating that at most sites within its range, this species co-occurs with distantly related species, in species-rich sites with high phylogenetic diversity.

Species with intermediate range sizes (Fig 2.4b and c) show variable frequency distributions for all metrics analyzed. For example, the white-tailed titi (*Callicebus discolor*) co-occurs with an average of 10.9 species (SR_{var} = 7.07), with its frequency distribution showing negative skew. Sites of high species richness were located along the eastern edge of its range, in areas of high species relatedness (low MNTD). Mean MPD was relatively high, with low variance and negative skew, while MNTD presented positive skew, evidencing high levels of relatedness of species in these sites. A larger species, with intermediate range size, the white-cheeked spider monkey (*Ateles marginatus*) exhibits far lower mean species richness (6.81, *var*. 2.89) and positive skew, indicating it occurs at sites with lower than average species richness. Frequency distributions of phylogenetic metrics show high MPD and MNTD values, with negative skewness, showing that the internal structure of this range reflects high phylogenetic diversity, with low relatedness of species.

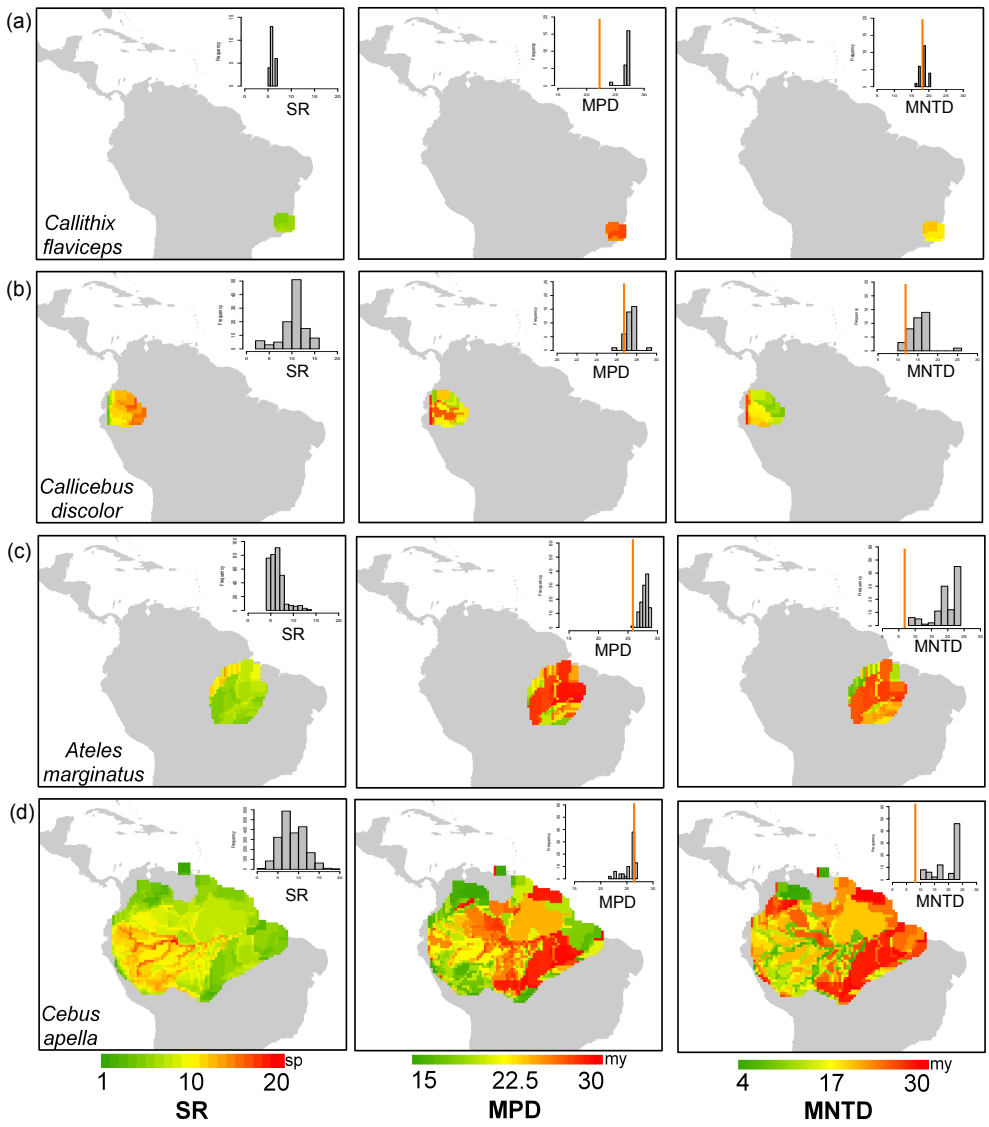

Figure 2.4. Frequency-distributions (histograms) and spatial distribution (maps) of species richness and phylogenetic metrics for four species of neotropical primates representing different quartiles of range size and body size. *(a) Callithrix flaviceps* (350 g)*; (b) Callicebus discolor* (1000 g); *(c) Ateles marginatus* (5900 g)*; (d) Cebus apella* (3000 g). Maps show species-richness (left), MPD (middle) and MNTD (right) values of sites within the distributional range of each species, and histograms show the frequency distribution of species-richness (left), MPD (middle) and MNTD (right). Orange lines on MPD and MNTD histograms represent species-specific phylogenetic field values based on the total set of co-occurring species within a focal species range (MPD_{sp} and $MNTD_{sp}$) that summarize the degree of phylogenetic relatedness among species within a range. Scales are comparable across species, but not across metrics. Maps were created using Arc-GIS 9.3 (ESRI, 2008).

Diversity fields of species with large ranges tended to resemble the pattern for the whole assemblage. The black-tufted capuchin (*Cebus apella*, Fig 2.4d) has a wide distribution, ranging across low to intermediate richness areas (SR_{mean} = 9). Its frequency distribution presents a large

variance of 8.49, and a small, but positive skew. MPD shows a longitudinal gradient, increasing towards the center of the range and decreasing towards east and west boundaries of the range. Areas of high phylogenetic relatedness (low MNTD) coincide with the location of large rivers, creating the negative skew observed in the FDs of the phylogenetic metrics. In most sites, the phylogenetic distance is large, with most sites being composed of distantly related species (high MNTD).

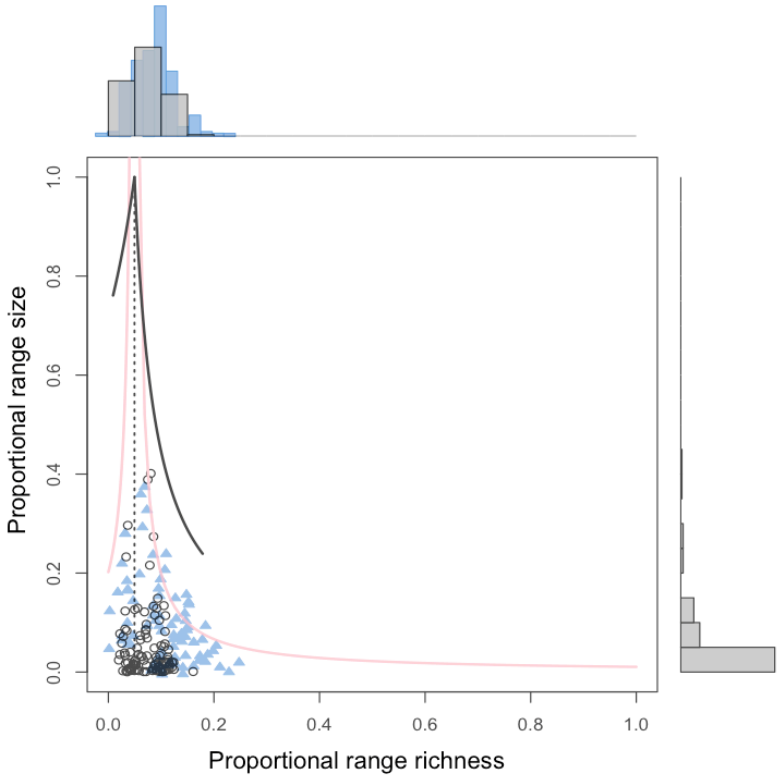

Figure 2.5. Range–diversity plot for 108 species of neotropical primates. Species are plotted based on their proportional range size (ordinate) and the proportional species richness within their range (abscissa). Histograms on top and on the right-hand side represent frequency distributions of proportional range richness and proportional range size, respectively. Solid curved line defines maximum mathematical limits for points given by the fill of the matrix. Vertical dashed line corresponds to mean proportional species richness of the PAM ($\bar{s}^*=f^*$), and pink hyperbolic curves represent lines of equal covariance among species. Black circles represent species in empirical PAM, and blue triangles correspond to the species under the null model of cohesive ranges using the spreading-dye algorithm. This null model retains the empirical range-size frequency distribution (right-hand side histogram), but changes species richness frequency distributions (top histogram in blue shade).

Range-diversity plots – Average richness within species ranges (s_i) varied widely for species with small ranges (s_i = 3.08 to 18 species). These species represented the points at the bottom of the range-diversity plot in Fig. 2.5. The location of most species points in this plot was constrained to approximate mean richness values (f^* line) by the distribution of widespread

species, such as brown-tufted capuchin monkey (*Cebus apella* $s_i = 9.01$) and red- handed howler monkey (*Alouatta seniculus* $s_i = 8.36$). Fifty-three species (49%) had average species richness within their ranges higher than the overall mean ($s_i > 8.28$), corresponding to points to the right of the vertical dashed line in Fig. 2.5. Fifty-five species (51%), with variable range sizes (2-1508 quadrats), co-occurred on average with 8 or fewer species (lower left corner of the plot). Proportional species diversity for sites varied from 0.01 to 0.18, meaning that a given site harbors at most 18% of the total diversity of neotropical primates. These maximum and minimum proportional values determined the boundaries and the dispersion of points in the range-diversity plot (Fig. 2.5).

Species points were concentrated on the lower and right side of the range-diversity plot, revealing an overall positive association among species within their ranges. Widespread species are arranged following the vertical line of mean proportional species richness, so the average diversity inside their range is close to the average for the entire distribution of all neotropical primates. Species to the left of the *f** line are those with smaller ranges, which occur in low-diversity areas, corresponding to the extremes of distribution of neotropical primates (Fig 2.1a). Histograms show a distribution skewed to restricted species and species-poor sites, reflected in the low *f** value (0.05). Points that follow the lines of positive covariance correspond to species that co-occur with a high number of species.

Phylogenetic fields – Phylogenetic structure of co-occurring species within individual species ranges exhibited high MPD_{sp} and $MNTD_{sp}$ values. MPD_{sp} ranged from 16.06-26.72 my and $MNTD_{sp}$ varied between 4.47 and 27.9 my (see Table A2 in Appendix A). Analyzing frequency distributions of phylogenetic metrics (MPD and MNTD mean, variance and skewness) provided information regarding the internal phylogenetic structure of species ranges that was different from information generated by phylogenetic fields described by a single value (MPD and MNTD sp). This can be seen in Fig. 2.4, where species-specific phylogenetic field values (orange lines for MPD_{sp} and $MNTD_{sp}$) are overlaid on frequency distributions of mean MPD and MNTD obtained from analyses of the phylogenetic structure of all cells from a focal species range.

Certain attributes of diversity and phylogenetic fields exhibited phylogenetic signal (SR_{mean}, SR_{var}, MPD_{skew}, $MNTD_{mean}$ and $MNTD_{skew}$), indicating that closely related species are more similar than expected due to their shared history. *K* statistics for all other attributes were low, ranging between 0.11 – 0.65) showing their evolutionarily lability. Species phylogenetic fields showed significant relationships with attributes of species ranges and statistical parameters of richness and phylogenetic frequency distributions. MPD_{sp} showed a significant relationship with all variables except for skewness. MNTD was significantly correlated only with range size, number of overlapping ranges and variance of MPD and MNTD, although the associations were very low ($R^2_{adj} < 0.1$) (Table 2.1).

Table 2.1. Results of PGLS regressions between phylogenetic field values (MPD_{sp} and $MNTD_{sp}$), range size, co-occurrence, and frequency distribution parameters of SR, MNTD and MNTD. Lambda (λ), slope (β), adjusted coefficient of determination R^2_{adj} and P-value are presented for the regressions.

			MPD_{sp}		$MNTD_{sp}$	
	λ_{ML}	R^2_{adj}	*P-val*	λ	R^2_{adj}	*P-val*
Range size	0.325	0.148	<0.0001	0.203	0.061	<0.0001
# overlap. ranges	0.247	0.407	<0.0001	0.075	0.083	<0.0001
SRmean	0.128	0.391	<0.0001	0.506	-0.004	0.582
SRvar	0.285	0.265	<0.0001	0.204	-0.01	0.977
SRskew	0.162	-0.003	0.523	0.161	-0.01	0.871
MPDmean	0.176	0.334	<0.0001	0.191	0.01	0.125
MPDvar	0.211	0.108	<0.0001	0.285	0.104	<0.0001
MPDskew	0.457	0.037	0.007	0.412	-0.001	0.993
MNTDmean	0	0.14	<0.0001	0.121	-0.001	0.412
MNTDvar	0.285	0.104	<0.0001	0.685	0.113	<0.0001
MNTDskew	0	0.031	0.055	0	0.027	0. 070

λ_{ML} maximum likelihood estimate of lambda to evaluate phylogenetic signal under a model of Brownian motion. Varies from 0 to 1, where 0 corresponds with the complete absence of phylogenetic structure and 1 means that variation in the trait is perfectly correlated with phylogeny.

Comparisons with cohesive-range null model – Given that the null model retained the empirical range size frequency distribution (*i.e.* row sums), average range size of species was the same as that of empirical values in all simulations. Range–diversity plots created based on simulations using cohesive ranges present a pattern similar to empirical data (blue triangles in Fig 2.4). Mean species richness for the region was higher, but presented a similar unimodal distribution ($SimSR_{mean}$ = 7.61; $SimSR_{var}$ = 12.82 - average of the 100 simulations). Simulated species showed a tendency to arrange more to the right of the mean proportional species richness line, showing higher covariance among species than in empirical distributions. Mean range-richness for the simulated species was 10.42 +/- 9.6. The histogram of range-richness values showed a peak to the right of *s** for the simulated data (Fig 2.4 top blue histogram).

Comparisons between observed patterns and null model simulations of phylogenetic fields showed higher values of MPD_{sp} and $MNTD_{sp}$, that could be a result of the shift in frequency distribution of richness values towards higher range-richness values observed in diversity fields. However, species' observed MPD_{sp} and $MNTD_{sp}$ values were well within the 95% confidence intervals of the simulated values, showing there were no significant differences in species phylogenetic fields once dispersal limitation is taken into consideration. Species that showed significant differences in their observed phylogenetic fields, had intermediate to small range sizes, and were principally endemics (*e.g. Leontopithecus rosalia, Oreonax flavicauda,*

Ateles fusciceps, Brachyteles arachnoides, Callicebus olallae). These presented lower than expected $MNTD_{sp}$ values, which suggests more overdispersion within simulated ranges when compared to empirical distributions. Species that showed significantly higher MPD_{sp} values when compared to the null distribution were distributed in the Amazon basin (*e.g. Callithrix pygmaea, Pithecia monachus, Ateles paniscus*), suggesting they co-occurred with more species than expected; however, no clear pattern emerged for the entire clade.

Discussion

Evaluating geographic co-occurrence patterns allows the understanding of species distribution by examining the within range variation in diversity patterns. Results here suggest that primate assemblages within individual species ranges are more species rich than expected based on the overall distribution of the taxon across the neotropics. Variation in phylogenetic signal found for attributes of species diversity and phylogenetic fields challenges the notion that ecological traits, such as geographic range size, are labile (Gittleman *et al*., 1996; Gaston & Blackburn, 1997). Lastly, results of null model analyses of range cohesion support the importance of dispersal limitation in the distribution of primate species, particularly for large ranging species.

Patterns of species richness and range size of neotropical primates follow those described for most tropical taxa, with a latitudinal gradient in species richness (Jetz & Rahbek, 2002; Davies *et al*., 2011) and a positive skew in range size frequency distribution (Brown *et al*., 1996). Phylogenetic patterns reveal areas of high endemism around the Amazon basin and its tributaries, as well as in Atlantic forest. Cells across these areas present low MNTD values, indicating high levels of relatedness between co-occurring species. MPD on the other hand shows a fairly homogeneous pattern, with high phylogenetic diversity across most of the domain, and a decrease at the northern and southernmost extremes of distribution. MPD patterns may be associated with a high level of turnover that exists in neotropical primate assemblages, where species-rich sites across the entire region are composed of different species, but from the same genus.

Range diversity plots – Attributes of species diversity fields are correlated with multiple properties of the location, environment and biogeographic history of the domain (*i.e*. area, isolation, latitude, longitude, elevation, temperature, precipitation, productivity, age), as well as life-history and ecological traits of species. Points on the range-diversity plot located to the left of the line of average proportional species richness for all quadrats (*f**) corresponded to species with small range sizes and low species richness. These are geographically restricted species, that occur along the borders of distributions in areas of low productivity, which can only support small assemblages (Kay *et al*., 1997). The cloud of points corresponding to the peak of range-richness in the top histogram in figure 2.5 correspond to species in the amazon basin, that have relatively small range sizes, but occur in highly productive areas, where many niches are available (Peres & Janson, 1999). The few points representing species with large proportional range size and range-richness close to the average for the entire matrix correspond to widespread

species (*Cebus apella, Alouatta seniculus*, *Saimiri sciureus*), which are more generalists, that allows them to occur in sites with high or low productivity, co-occurring with a wide array of species across their distribution.

Species showing low species richness within their ranges (low s_i*) differ in composition (*i.e*. identity) in relation to where their range is located in the domain. Ranges of species at northern latitudes typically encompass a few generalist species that have been able to colonize forests of Central America and southern Mexico (*Alouatta palliata, Cebus capuchinus*). These subtropical areas present multilayered forests that are less vigorous than tropical forms, because of pronounced seasonal temperature regimes (Archibold, 1995), which might prevent species from being as densely packed in niche space as they are in tropical areas (Safi *et al*., 2011). In contrast, species in the southernmost extent of distribution that present low range-richness values correspond to endemic species occurring in sites of low productivity that allow for few species to co-occur at a site (*Alouatta coibensis, Cebus nigritus*). This pattern is opposite to what Villalobos & Arita (2010) find for phyllostomid bats, in which species occurring at northern latitudes are endemics with comparatively small ranges, and those in the southern latitudes are species with very large ranges, occurring at species rich and species poor sites throughout their distribution. These differences may be attributed to significant differences in dispersal abilities of these two taxa (Schloss *et al*., 2012), as well as differences in diversification and colonization dynamics of these clades (Bininda-Emonds *et al*., 2007).

Unlike range diversity plots for birds (Borregaard & Rahbek, 2010) and phyllostomid bats (Villalobos & Arita, 2010) in the neotropics, primates do not show the characteristic cloud of points extending towards the region of the range diversity plot that corresponds to species with small range size, that occur in highly diverse sites. For bats and birds, these sites of extremely high diversity correspond to species endemic to the Andes (Graves & Rahbek, 2005; Rahbek *et al*., 2007) where many clades have diversified (Fjeldså *et al*., 2012). For neotropical primates, endemism is high (evidenced by low MNTD values) across the Amazon basin, where multiple barriers are present that promote speciation (Ayres & Clutton-Brock, 1992). Thus, disparities in the location of clouds of points in range diversity plots between taxa (birds, mammals and primates) can be explained by combined effects of habitat heterogeneity and differences in the evolutionary history of these clades.

Inferences from diversity and phylogenetic fields – Examining frequency distributions of richness and phylogenetic metrics allows a deeper investigation into possible mechanisms contributing to the internal structure of ranges. For instance species occurring only in species-poor sites could be considered poor competitors ("super tramps" *sensu* Diamond, 1975), precluded them from inhabiting sites of high species richness. However, if low species richness is accompanied by low MPD and MNTD values, as is the case for some species of tamarins, capuchins and howlers inhabiting Atlantic Forest, competition may not be the driving mechanism structuring their ranges. Rather, high local speciation rates (Cardoso-daSilva & Oren, 1996) coupled with environmental filtering may promote co-occurrence of few closely related

species throughout their range of distribution (Cavender-Bares *et al*., 2009). On the other hand, species with small range sizes, which occur only in species-rich sites with high MPD_{sp} and $MNTD_{sp}$, may possibly be identified as more generalist forms capable of co-occurring with many other species. Certain species of tamarins, titis and squirrel monkeys present this pattern. These are all considered more generalists/ omnivore species (Kinzey, 1997), that can change their primary food sources depending on seasonal availability, and thus avoiding competition.

Overall, phylogenetic relatedness of a species with its co-occurring assemblage is related to attributes of its diversity and phylogenetic fields. Significant relationships were found between MPD_{sp}, range size and parameters of frequency distributions (mean and variance of SR, MPD and MNTD). MPD increased with species richness for species with negatively skewed frequency distributions. Species showing high range-richness also had high MPD and high MNTD values. Conversely, species co-occurring with fewer species (normal, or positively skewed species richness frequency distributions) show varying levels of phylogenetic relatedness. These differences in the strength and direction of the association may reflect the complex history of diversification, extinction and dispersal of this group of species. For instance, recent colonization events coupled with fast adaptive radiation (and high interspecific competition) may also result in low levels of phylogenetic diversity (MPD) across ranges of species that otherwise occur in highly diverse sites, with closely related species (low MNTD). Significant correlations were found between range size and MPD_{sp} /$MNTD_{sp}$ These patterns however varied in relation to the location of a species' range across the domain. Such variability suggests that different mechanisms may be operating to structure species ranges.

An interesting finding of this study is the presence of phylogenetic signal in certain attributes of species diversity and phylogenetic fields. Recent tests of range size heritability found a weak phylogenetic signal in the range sizes of mammals, suckers (fish), and parrots (Freckleton *et al*. 2002). Phylogenetic signal for range size and its internal structure attributes probably arise due to range size heritability, where the ancestor's range size is passed on to descendants at speciation (Borregaard *et al*., 2012). Small ancestral ranges are thus likely to give rise to two small descendant ranges. Likewise, ancestors with large ranges may give rise to at least one large-ranged descendant. Differences in sister species' range sizes may be due to asymmetrical vicariance events (Gaston & Chown, 1999) or range changes after speciation (Losos & Glor, 2003).This phylogenetic signal may explain the high levels of correlation among attributes of species' phylogenetic fields observed in these analyses.

Inferences from null models – Contrasting observed patterns against null expectations represents the main strategy for assessing the significance of patterns and relating these to underlying theory (Gotelli & Graves, 1996). The null model used here does not allow for discontinuities in species geographical ranges, thereby incorporating the effects of geometric constraints and range cohesion (Arita & Rodriguez-Tapia, 2009; Colwell *et al*., 2009). This constraint reflects biologically realistic processes that limit range expansion, particularly dispersal limitation (Hubbell, 2001). Results of null model simulations show that range-

cohesiveness generates higher association between species than that observed for empirical data. This is reflected by a higher average value for simulated range-richness. These results suggest that while dispersal limitation may be a significant force structuring neotropical primate species distribution, other factors may be acting to reduce species association. These may be related to competitive interactions and ecological requirements of species, as well as to the biogeographic history of the region.

In the range-diversity plot, species simulated based on the spreading-dye algorithm show a high overlap with the observed location of species, particularly in the central part of the range-diversity plot; however, species towards the periphery of the mathematical constraint zone do not overlap with those of the simulation. These results are similar to those of Villalobos & Arita (2010) and Soberón & Ceballos (2011) evaluating diversity fields of phyllostomid bats and dispersion fields of mammals across the globe, respectively. Species points that do not overlap with the randomized values commonly correspond to species showing extreme mean range and mean richness values. These are endemic species with small ranges, occurring in highly diverse sites, such as golden lion tamarins, muriquis and brown-headed spider monkeys, which all represent species of high conservation concern (IUCN, 2012). Phylogenetic field analyses showed similar results as those for diversity fields, with most empirical phylogenetic fields not differing from random expectations. These results are similar to Villalobos *et al*. (2013a) findings for phyllostomid bats in the Neotropics; the only study of phylogenetic fields available. Here the authors relate this random pattern in phylogenetic fields to niche conservatism, a process known to influence the distribution and diversity patterns of this taxon (Stevens, 2006; 2011). This may also be the case with neotropical primates, where most species share similar environmental preferences owing to their tropical origin and diversification within the same geographic domain (Rosenberger *et al*., 2009). This would allow them to occur in the same regions with closely and distantly related species, producing phylogenetic fields indistinguishable from range size variation alone.

Conclusions – Neotropical primates present patterns of positive association across their ranges. Evaluating at species frequency distributions it can be inferred that patterns of species co-occurrence change in relation to species range size as well as to the location of species ranges across the domain. Furthermore, evaluating range diversity plots it can be observed that most species present small range sizes, but vary widely regarding richness values within their distributions. These relationships allowed identification of endemic species living in highly diverse areas as well as those present in more seasonal environments such as Atlantic Forests. Lastly, neotropical primates show a lower level of co-occurrence than expected from a range-cohesion null model, which suggests that dispersal limitation may not be the only factor influencing species distribution and patterns of association. Phylogenetic diversity fields analyses showed that neotropical primates co-occur frequently with closely related species, particularly in areas of high species richness (e.g. Amazon basin). Spatial distribution of MPD and MNTD values for species with differing range sizes evinced complex patterns, which are largely dependent on the size, shape and location of the geographic ranges. MPD_{sp} and $MNTD_{sp}$

values showed a lot of variation, with many species presenting high values across their range, which suggests low clustering in assemblages. I find significant phylogenetic signal in many of the attributes used to describe species diversity and phylogenetic fields, which supports the premise that this approach provides further insights into analyses of species distributions and patterns of association, than when these are investigated independently. While here I focus on describing patterns, the next step is to create testable hypotheses regarding the influence of historical, spatial and environmental (present, past and future) processes creating changes in the internal structure of species ranges. Pattern-oriented modeling, as in a general simulation model (GSM) proposed by Gotelli *et al*. (2009) and spatially explicit species assemblage modeling (SESAM, Guisan & Rahbek, 2011), that allow inclusion of processes such as speciation, dispersal and extinction in a heterogeneous landscape are expected to provide mechanistic explanations regarding species distribution and co-occurrence. Furthermore, exploring effects of life-history (life-span, dispersal ability), ecological (diet) and morphological traits (body size) on information generated from diversity fields will allow inferences regarding ultimate mechanisms generating diversity patterns.

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CHAPTER 3. ROLE OF ENVIRONMENTAL, HISTORICAL AND SPATIAL PROCESSES IN THE STRUCTURE OF NEOTROPICAL PRIMATE COMMUNITIES: CONTRASTING TAXONOMIC AND PHYLOGENETIC PERSPECTIVES[1]

Introduction

Understanding processes underlying patterns of species coexistence and community structure remains a central goal of ecological research. Mechanisms proposed to explain these patterns at local and regional scales have generally been divided into three general categories. Deterministic theories suggest that niche-based processes, such as interspecific interactions, environmental filtering and differences in niche requirements among species, determine patterns of diversity and composition of communities (Tuomisto *et al*., 2003). In contrast, historical theories suggest that geologic and evolutionary processes, such as vicariant events (*e.g*. mountain uplift, river formation, refuge areas during climatic fluctuations, etc.) or variation in rates of diversification and extinction are important determinants of species distributions and hence, community structure (Ricklefs, 1987). Lastly, stochastic processes, such as ecological drift, dispersal limitation and differential colonization/extinction dynamics, can control local community structure (Hubbell, 2001). Unfortunately different mechanisms can generate similar spatial patterns, requiring decoupling of their independent effects to obtain a clear understanding of their relative roles in shaping patterns of diversity. Recently ecologists have begun to address the importance of explicitly investigating spatial structure in community studies, acknowledging that its presence indicates an underlying process that may have gone unnoticed (Peres-Neto *et al*., 2006; Dormann *et al*., 2007). For instance, variation in environmental conditions through species-habitat associations can create spatial structure across communities, whereby environmental variables are spatially structured, and species distributions reflect this structure through induced spatial dependence (environmental control, Tuomisto *et al*., 2003). In addition, processes endogenous to species assemblages can also create spatial structure (*i.e*. dispersal limitation generates aggregated spatial patterns [Hubbell, 2001]), leading to spatial autocorrelation in species data. A promising statistical approach to assess simultaneously the relative contribution of different mechanisms structuring communities is variation partitioning (Borcard *et al*., 1992; Peres-Neto *et al*., 2006). Such an analysis quantifies variation in community composition that is uniquely attributable to different predictor matrices (*e.g*. environment, history, space) after controlling for their shared effects, allowing inferences regarding relative influence of potentially competing mechanisms that may have independent and complementary or redundant effects (Tello & Stevens, 2010).

The degree to which deterministic, historical and stochastic processes are responsible for

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current patterns of community structure may not be able to be inferred from taxonomic information only. This is because species taxonomic identities alone do not reflect critical information regarding evolutionary or ecological similarity of species (Webb, 2000; Pavoine & Bonsali, 2011). In recent years community ecology has seen a growing interest in incorporating phylogenetic information to provide a historical framework for quantifying the role of historical, biogeographic and evolutionary processes in structuring communities (see reviews in Webb *et al*., 2002, Cavender-Bares *et al*., 2009, and references therein). The objective of these phylogenetic methods is to infer processes affecting assembly such as environmental filtering or competition based on patterns of relatedness among co-occurring species (Webb, 2000). Given the assumption that traits are phylogenetically conserved within species groups, closely related species are expected to have greater niche similarity (Webb *et al*., 2002). Thus, if the environment is acting as a filter on community assembly then closely related species are expected to co-occur more commonly than distantly related species (phylogenetic clustering). In contrast, given that competition is expected to be more intense among closely related species due to their niche similarity, such interactions are expected to limit coexistence, selecting for sets of phylogenetically less related species that co-occur in local communities (phylogenetic over-dispersion). These different patterns of community structure can be investigated by comparing mean phylogenetic distance (MPD) or mean nearest neighbor phylogenetic distance (MNTD) of species present in local communities to communities assembled at random from a regional species pool (Webb *et al*., 2002). Furthermore, investigating spatial variation in measures characterizing evolutionary history such as phylogenetic diversity (PD; Faith, 1992) also allows for predictions regarding changes in diversification rates underlying ecological and evolutionary hypotheses of diversity (Davies *et al*., 2007). To date few studies have compared taxonomic and phylogenetic perspectives when analyzing patterns of community structure (but see Gomez *et al*., 2010, Pavoine & Bonsali, 2011). Few findings that exist highlight the promising information that is provided by assessing simultaneously different aspects of diversity. For instance, communities with similar phylogenetic community structure may differ in their species composition and vice-versa. Analyses of taxonomic or phylogenetic community structure alone cannot fully address how physiological limitations, biotic interactions, geographic barriers and evolutionary processes interact to influence local community structure (Gomez *et al*., 2010). In fact, patterns of phylogenetic structure of communities may not only reflect niche-based processes such as competition and habitat filtering, but also evolutionary and biogeographic processes (Cavender-Bares *et al*., 2009; Kembel, 2009). For instance, low dispersal rates across regions and high levels of speciation within regions may lead to phylogenetic clustering rather than environmental filtering alone (Webb *et al*., 2002; Cavender-Bares *et al*., 2009; Gomez *et al*., 2010).

Neotropical primates represent an ideal group for examining patterns of diversity and coexistence in natural communities. They are a monophyletic, highly diverse clade (>150 species; Groves, 2005) which present some of the most species rich communities for the entire order. This radiation is widely distributed across tropical and subtropical forests from southern Mexico to northern Argentina. New World primates vary greatly in body size, diet, social

structure, microhabitat use and foraging behavior, which allow them to diverge on several axes of their ecological niche (Fleagle, 1999). Consequently, these species are differentially sensitive to environmental factors such as temperature and seasonality of food availability (Kay *et al*., 1997; Peres & Janson, 1999). Furthermore, extant primate communities are the result of multiple events of historical dispersal and vicariance from three provinces of origin (Atlantic, Amazonian and Patagonian; *sensu* Rosenberger *et al*., 2009) which in turn were affected by different historical and biogeographic events such as the presence of riverine barriers, mountain uplifts and forest fragmentation during the last glacial period (see Haffer, 1997 and references therein). Here, we integrate information on species composition and phylogenetic diversity and structure with multiple predictors representing potential mechanisms governing community assembly (environmental variation, historical barriers, and spatial variables reflecting dispersal limitation) to determine their relative contribution to explaining current structure of neotropical primate communities.

To the best of our knowledge, only two studies have simultaneously incorporated environmental and evolutionary factors into analyses of primate community structure (Kamilar, 2009; Beaudrot & Marshall, 2011), and none has directly tested the effects of explicit historical processes, nor the influence of the three mechanisms simultaneously. While analyses of phylogenetic community structure for primates have been undertaken recently (see Cardillo *et al*., 2008; Cooper *et al*., 2008; Kamilar & Guidi, 2010), ours is the first study that directly attempts to characterize phylogenetic community structure in relation to different mechanisms proposed to structure natural communities. We evaluated how variation in taxonomic and phylogenetic community structure of neotropical primates corresponds to environmental, historical and spatial predictors to determine whether similar processes are responsible for patterns of different components of biodiversity. If niche based processes (*e.g*. niche availability, species-habitat associations, or physiological limitations driven by environmental conditions) structure neotropical primate communities, we would expect that the proportion of variation in community structure explained by environmental variables to be greater than that of historical and spatial variables. Furthermore, we expect this fraction to remain significant even after partialling out variation correlated with historical and spatial variables. On the other hand, if historical processes are more important determinants of primate community structure we would expect that the proportion of variation explained by these predictors to be greater than that explained by environmental and spatial variables, and that this fraction will remain significant even after controlling for effects of environmental gradients and spatial variation. Lastly, if primate community structure were the result of dispersal-based structuring processes, we would expect that the proportion of variation explained by spatial variables to be greater than that of environmental and historical predictors. Furthermore, spatial variation should remain high and significant even after accounting for environmental and historical effects.

Methods

Data for seventy-four communities with known primate species composition were obtained from the literature (Figure 3.1). These communities were selected so as to control for differences in sampling effort and census techniques (See Appendix B for a description of selection criteria). All biomes inhabited by neotropical primates are represented in our sampled communities (Fig. B1 in Appendix B). Species belonging to the genus *Aotus* (owl monkeys) were not included because their nocturnal habits makes their observation difficult and hence their presence-absence data unreliable.

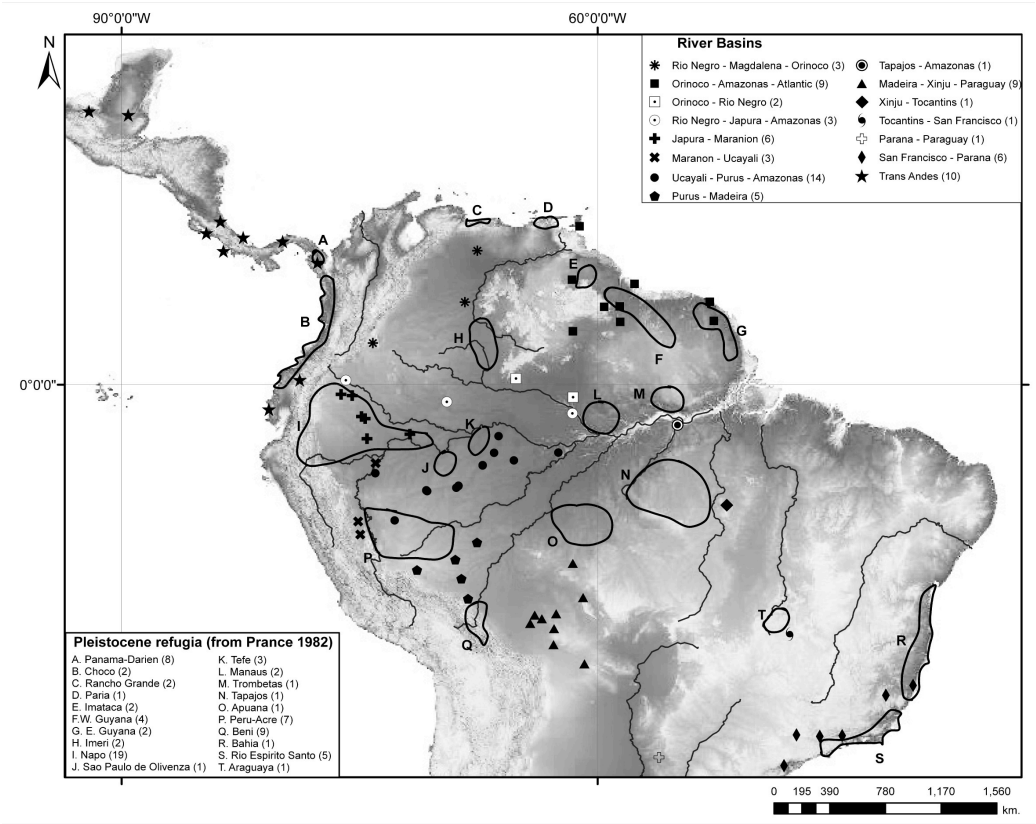

Figure 3.1. Location of communities included in analyses. Symbols in map legend represent assignment of communities to different river basins. All sites in Central America, and the western Andes were assigned to the "trans-Andes river basin". Letters represent proposed Pleistocene forest Refugia. Number in parentheses represents the number of communities assigned to each river basin and forest refugium. Names of Refugia (from Prance 1982): **A**-Panama-Darien (8); **B**-Choco (2); **C**-Imeri (2); **D**-Napo (19); **E**-Tefe (3); **F**-Sao Paulo de Olivenza (1); **G**-Peru-Acre (7); **H**-Beni (9); **I**-Rio Espirito Santo (5); **J**-Bahia (1); **K**-Araguaya (1); **L**-Apuana (1); **M**-Tapajos (1); **N**-Manaus (2); **O**-Trombetas (1); **P**-Eastern Guyana (2); **Q**-West Guyana (4); **R**-Imataca (2); **S**-Paria (1); **T**-Rancho Grande (2). (See Table B1Appendix B for references to community numbers and their sources; see Appendix B Table B2 and B3 for list of assigned communities to individual refugia and river basins respectively).

The phylogeny used to calculate metrics of phylogenetic diversity was obtained from Fabre *et al*. (2009), based on the taxonomy of Groves (2005). This is a large-scale dated supermatrix phylogeny of primates derived from a combination of mitochondrial and nuclear DNA markers. Species identifications obtained from the literature were synonymized to match this taxonomy. We performed our analyses using other published phylogenies but chose this one because it represented the most species present in our communities, and presents few unresolved nodes. However, results did not differ much when using other phylogenies, and the level of correlat ion between phylogenies for all phylogenetic diversity metrics used in our analyses was high for most metrics (R^2 mode = 0.92; See Fig. B2 in Appendix B).

Four different metrics were used to characterize phylogenetic structure of communities. All metrics are based on branch lengths of the phylogeny, and represent measures in millions of years of divergence from a common ancestor. *Phylogenetic diversity* (PD) characterizes overall evolutionary history represented by species in a community (Faith, 1992). *Average taxon age* (ATA) quantifies the average age of species in millions of years in a community. In addition, we incorporated measures that estimate phylogenetic community structure by assessing pairwise relationships among species in communities (*mean nearest taxon distance*-MNTD and *mean pairwise distance*-MPD; Webb, 2000). Phylogenetic community structure measures were not standardized with respect to a regional species pool, as the objective of our work was not to determine whether over-dispersion or clustering exists (see Kamilar & Guidi, 2010 for these results), but rather to determine how such patterns of phylogenetic relatedness of co-occurring species are explained by ecological, historical and spatial mechanisms. Collinearity between these measures was relatively low (Pearson's correlation ranges from 0.11 to 0.73; Fig.B3 in Appendix B), thus we are confident these measures reflect complementary aspects of the phylogenetic component of biodiversity. Phylogenetic metrics were computed using packages Ape (Paradis *et al*., 2004) and Picante (Kembel *et al*., 2010). All analyses were conducted in R, version 2.10 (R Development Core Team, 2009).

Environmental, historical and spatial predictors— Nine environmental predictors representing variation in climate and energy (net primary production, NPP) were selected based on their biological relevance to primates (Kay *et al*., 1997; Peres & Janson, 1999), while also attempting to minimize redundancy (See Table B4 in Appendix B for correlation matrix): net primary productivity, minimum average yearly temperature, maximum average yearly temperature, mean annual temperature, temperature seasonality, minimum average annual precipitation, maximum average annual precipitation, total annual precipitation, and precipitation seasonality. Many of these variables are used in analyses of broad scale diversity patterns (see Hawkins *et al*., 2007; Kamilar, 2009; Stevens, 2011). Environmental information was gathered from WorldClim (Hijmans *et al*., 2005) and NPP from Imhoff *et al*. (2004). Values used represent the average value of the focal cell – each community's spatial coordinates – and its surrounding cells in order to obtain a more accurate representation of mean climatic conditions of the local area. Resolution of raster maps for environmental variables and NPP was 0.25°.

We selected variables to represent two historical hypotheses that take into consideration roles of dispersal and vicariance in shaping tropical species distributions: the riverine barriers hypothesis and the Pleistocene forest refugia hypothesis (see Haffer, 1997). Communities were ascribed to a matrix of dummy variables representing one of 15 river basins or 20 forest refugia (Fig. 3.1) using GIS operations performed in ArcGIS 9.3 (ESRI, 2008; See Appendix B for a description of the methodology used for assignment of communities and the respective correspondence of communities to each river basin and Pleistocene refugia, Table B2 and B3 respectively). Principal components analyses (PCA) were used to reduce the dimensionality of environmental and historical matrices, as well as to avoid multicollinearity among variable suites, which artificially increases explained variation (Legendre & Legendre, 1998).

Spatial variables representing dispersal-based structuring processes were incorporated into a predictor matrix using spatial analyses. Spatial structure in our data set was represented by eigenvectors derived from principal coordinates of neighbor matrices (PCNM) based on the geographic coordinates of communities (Borcard *et al*., 2004). PCNM vectors are obtained by eigenvalue decomposition (principal coordinates analysis) of a truncated matrix of distances among sites. Positive PCNM eigenvectors were retained for further analysis. Spatial analyses were performed using package Vegan (Oksanen *et al*., 2009) and packfor (Dray *et al*., 2006) in R.

Statistical analyses— Redundancy analysis (RDA) and partial RDA were chosen for variation partitioning analysis (Borcard *et al*., 1992) because preliminary ordination using detrended correspondence analysis (DCA) revealed short gradients in response matrices. Environmental and historical PCs and PCNM vectors were entered into the predictor matrices in a forward stepwise fashion with an alpha level of 0.05, retaining only those that significantly contributed to the explanation of response matrices of taxonomic and phylogenetic structure. Variation partitioning analyses quantify amount of variation in a response matrix (community structure) attributable to different combinations of explanatory datasets, in our case, environmental, historical and spatial (Borcard *et al*., 1992; Legendre & Legendre, 1998). Total variation explained by the three types of explanatory variables (environment, history, space) was decomposed into eight components (Fig. 3.2).

Additionally, we estimated the total amount of variation associated with each set of predictors without partialling out the effects of the others. Significance of fractions was evaluated by comparing the adjusted coefficient of determination (R^2_{adj}) to those created from 10,000 permutations of the original data (Borcard *et al*., 1992; Peres-Neto *et al*., 2006). In addition we conducted permutation tests to estimate whether particular fractions were larger than expected by chance. These were done by permuting response matrices (taxonomic and phylogenetic) and using these randomly rearranged matrices to conduct variation-partitioning analyses. This procedure was replicated 1000 times generating a frequency distribution of adjusted R^2 values for each fraction expected under a null hypothesis of random association between response and predictor matrices. If the observed values of each fraction were greater

than the 95% quantile of their random distributions, then the component was considered to be statistically greater than expected by chance. R code to run these analyses can be found in Tello & Stevens (2010). These analyses were also carried out independently for each of the four different phylogenetic metrics to determine whether the influence of a particular predictor changes depending on the aspect of phylogenetic structure being investigated.

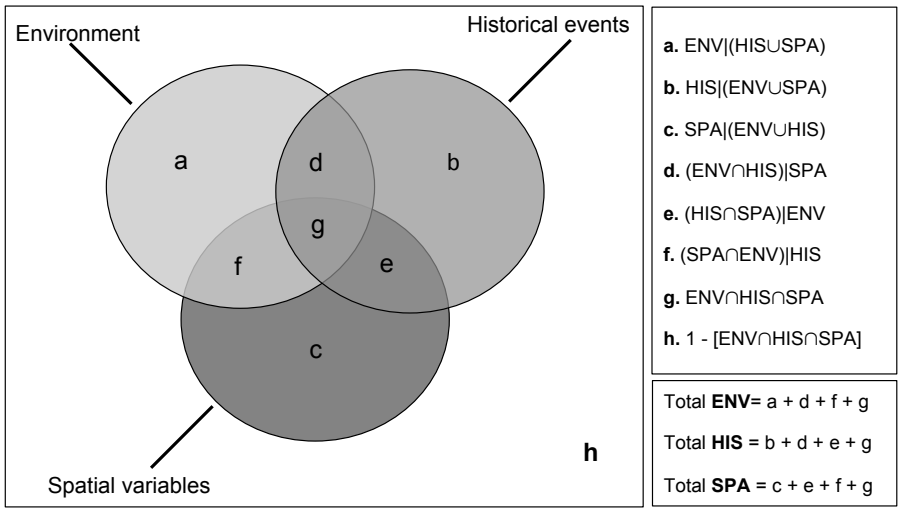

Figure 3.2. Schematic diagram of variation partitioning analyses and its corresponding fractions of variance explained. Variation in community structure was partitioned between environmental-ENV, historical-HIS and spatial-SPA predictors. Fractions a-c represent unique effects of each predictor, *i.e*. after controlling for effects of the other two predictors (**a.** pure effect of environment alone - ENV|(HIS∪SPA); **b**. pure effect of historical events alone - HIS|(ENV∪SPA); **c.** pure effect of spatial variation alone - SPA|(ENV∪HIS)). Fractions d-f represent variation explained by pairs of predictor sets after controlling for the effects of the remaining predictor (**d.** combined effects of environment and historical components - (ENV∩HIS)|SPA; **e.** combined effects of historical and spatial predictors -(HIS∩SPA)|ENV; **f.** combined variation of spatial and environmental variables -(ENV∩SPA)|HIS. Fraction **g** represents variation explained by all three predictors simultaneously-ENV∩HIS∩SPA. Finally, fraction **h** represents variation in community composition that is not explained by any of the analyzed predictors. ∩ intersection; ∪ union; | after controlling for.

Results

Sixty primate species were recorded across the 74 selected communities (Appendix B, Table B5). Sites exhibited considerable variation both in primate species richness and composition. Local species richness ranged from 2 to 13 with an average of 5.8 species, although species poor communities (<3 sp.) were far more common (Fig. B4a in Appendix B. Overall, most species occurred at only a few sites (Fig. B4b in Appendix B). Composition varied among communities with similar species richness. The most widely distributed species were *Cebus apella* (49 sites), *Alouatta seniculus* (44 sites), *Saimiri sciureus* (30 sites) and *Cebus albifrons* (28 sites). In contrast, 11 species were present in only one community each (Appendix B, Table B5). Species

rich communities (>6 sp.) were found around central-western Amazonia, close to the eastern Andean slopes (Fig. 3.3a).

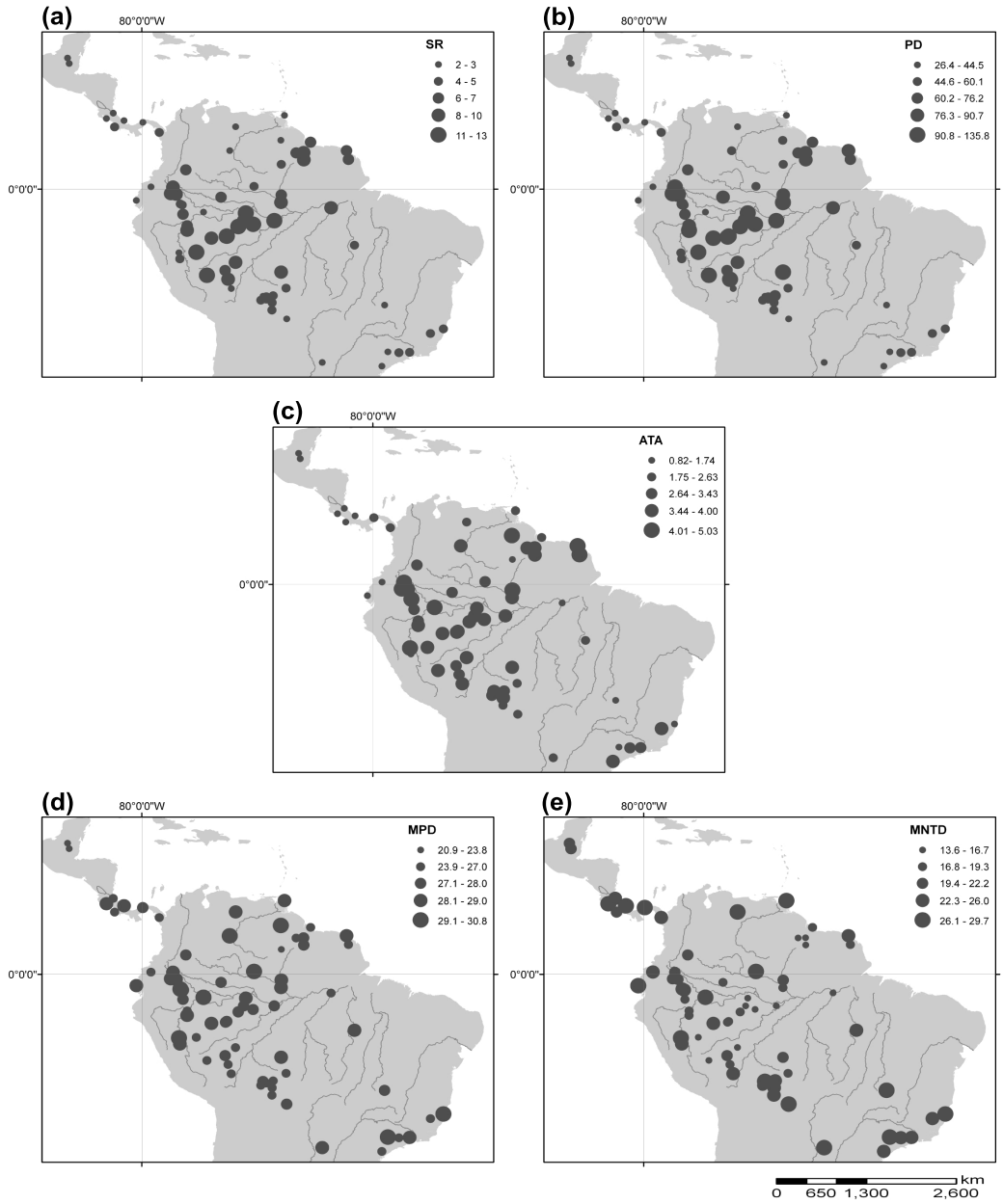

Figure 3.3 Spatial distribution of variation in species richness, phylogenetic diversity and structure in analyzed communities. Units for all phylogenetic metrics are millions of years (my). Size of the circles is proportional to values for each metric, with similar size scale to allow comparisons. (a) SR - species richness- (mean 5.8 sp.) (b) PD - phylogenetic diversity (mean 70.4 my.); (c) ATA - average taxon age (mean 3 my.); (d) MPD - mean pairwise distance (mean 27.6 my.) (e) MNTD - mean nearest taxon distance (mean 21.7 my.).

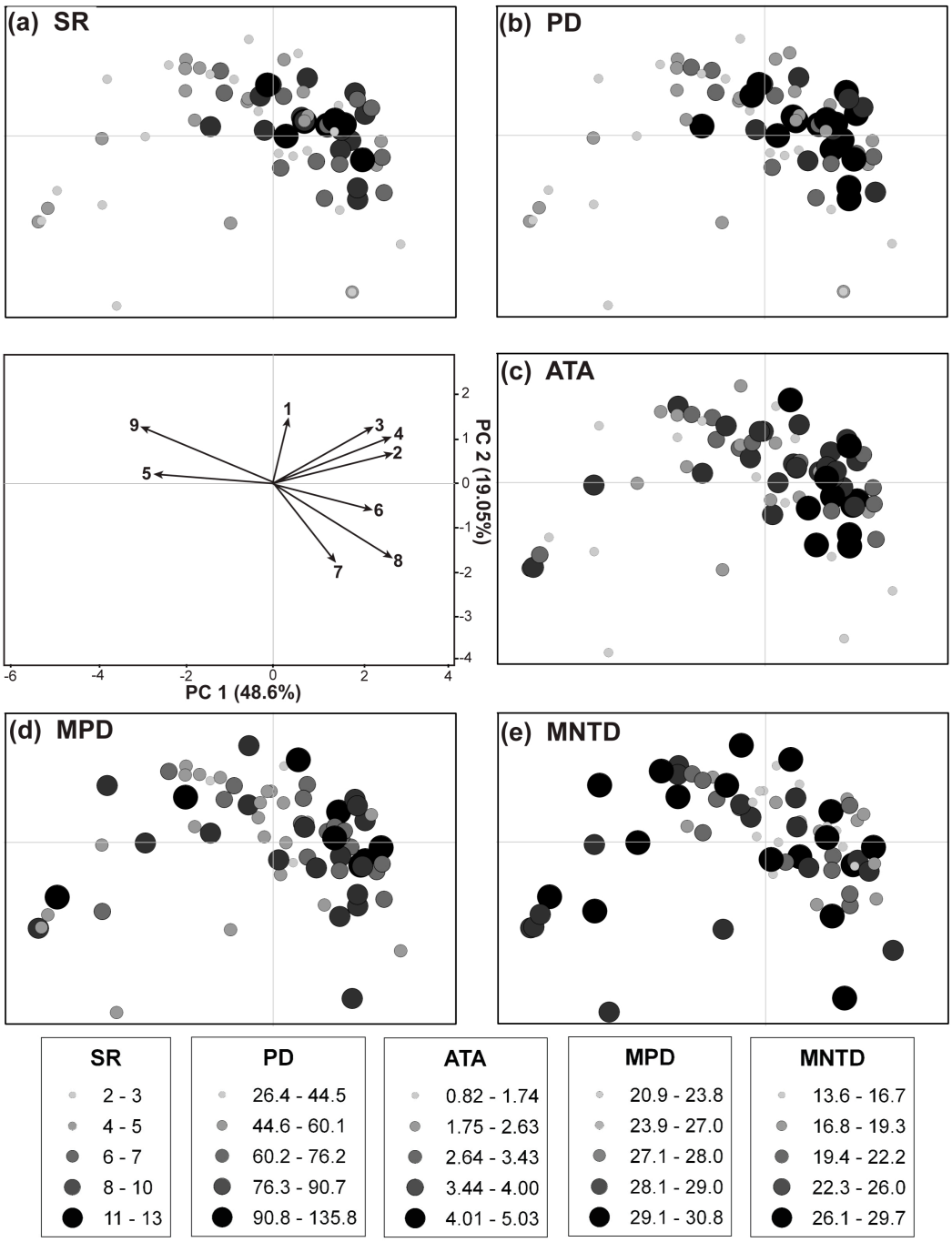

Figure 3.4. PCA based on climatic attributes of sampled communities reflecting the relationship of predictor variables (a) SR - species richness; (b) PD - phylogenetic diversity; (c) ATA - average taxon age; (d) MPD - mean pairwise distance; (e) MNTD - mean nearest taxon distance, with environmental variables: (1) net primary productivity; (2) minimum average yearly temperature; (3) maximum average yearly temperature; (4) mean annual temperature; (5) temperature seasonality; (6) minimum average annual precipitation; (7) maximum average annual precipitation; (8) total annual precipitation; and (9) precipitation seasonality.

Phylogenetic characteristics of communities were heterogeneously distributed across the Neotropics and varied depending on the particular metric. PD followed patterns of species richness, while MPD and MNTD exhibited far more complex spatial distributions. Species rich communities in the center of the primate distribution had higher PD values, while species poor communities presented low PD (Fig. 3.3b). For ATA, communities in central and western Amazonia are composed of younger species compared with those along the edges of the distribution of the clade, and communities at higher latitudes were composed of fewer, more distantly related species than communities at lower latitudes that contained a greater number of closely related taxa (*i.e.* central/western Amazonia; Fig. 3.3c). Communities nearby major river systems, such as those in the Amazon basin were represented by taxa that were more related (low MPD and MNTD) than communities not directly associated with river systems (Fig. 3.3d, e). Furthermore for MNTD, relatedness was lower (high MNTD values) at the extremes of the distribution of neotropical primates where communities are represented by fewer more distantly related species (*e.g.* capuchins and howlers or howlers and titis) while communities in the central and western Amazon are composed of more closely related species, and in many cases these are congeners (*e.g. Cebus*, *Saguinus*, *Callicebus*, *Callithrix*; Fig. 3.3e).

Principal components analysis (PCA) of environmental conditions across communities reflects the relationships between species richness and phylogenetic metrics and environmental gradients (Fig. 3.4). The X-axis of the PCA, which explains 48.6% of the variation, represents a seasonality, low temperature (correlated with low precipitation) gradient; while the Y axis, which explains 19.05% of the variation, represents productivity (correlated with high temperature and precipitation). More seasonal, less productive, drier and colder sites load negatively on both axes, while warmer, wetter, more productive sites load positively. Communities with high SR and PD are found in relatively warm, wet, productive sites, occurring in the right side of the ordination. Sites with high MNTD and ATA corresponding to productive, dry, warm lowlands on the extremes of the distribution of the taxon are at the left side of the ordination.

Variation partitioning— Total variation explained by the model that included all predictors was 49.3% for taxonomic structure and 66.8% for phylogenetic structure (Table 3.1 & 3.2 respectively). Variation partitioning analyses demonstrate that unique and shared contributions of predictor matrices differed, particularly when looking at the significance and relevance of fractions for phylogenetic metrics independently (Fig. 3.5a, b). In all analyses the most important fraction of independent variation was that of unique spatial effects (fraction c), explaining between 3 to 40% of variation). Independent historical effects (fraction b) were small (<11%) and significant only for taxonomic structure, ATA and MPD. Variation associated with independent environmental effects (fraction a) was extremely small (<4%) and significant only for taxonomic structure and ATA.

Much of the variation in taxonomic and phylogenetic composition associated with historical predictors is spatially structured (fraction e), explaining large and significant proportions of variation in all cases (9-16%; Table 3.1 & 3.2; Table B6 in Appendix B).

Table 3.1. Results of variation partitioning analysis of neotropical primate taxonomic community structure into unique (a-c) and shared fractions (d-g) explained by environmental (ENV), historical (HIS) and spatial (SPA) processes. Adjusted R^2 values in bold are statistically greater than expected based on permutation tests.

Names/fractions	Adjusted R^2	p-value	95% Confidence Intervals of adjusted R^2	
Environment (ENV)	**0.184**	**0.000**	0.207	0.326
Historical (HIS)	**0.360**	**0.000**	0.433	0.594
Spatial (SPA)	**0.402**	**0.000**	0.467	0.612
ENV∩HIS	**0.395**	**0.000**	0.514	0.695
ENV∩SPA	**0.422**	**0.000**	0.541	0.701
HIS∩SPA	**0.479**	**0.000**	0.666	0.850
ENV∩HIS∩SPA	**0.493**	**0.000**	0.755	0.960
Independent fractions:				
a- ENV|(HIS∪SPA)	**0.014**	**0.023**	0.060	0.149
b - HIS|(ENV∪SPA)	**0.070**	**0.007**	0.183	0.300
c - SPA|(ENV∪HIS)	**0.098**	**0.001**	0.189	0.332
Shared fractions				
d - (ENV∩HIS)|SPA	0.007	0.352	-0.058	0.027
e - (HIS∩SPA)|ENV	**0.141**	**0.000**	0.024	0.180
f - (ENV∩SPA)|HIS	0.021	0.123	-0.057	0.053
g - ENV∩HIS∩SPA	**0.142**	**0.000**	0.109	0.263
Unexplained variation				
h - 1–(ENV∩HIS∩SPA)	0.507	1.000	0.040	0.245

Note: (∩ intersection; ∪ union; | after controlling for).

Table 3.2. Results of variation partitioning analysis of neotropical primate phylogenetic community structure (combining all metrics: PD, ATA, MPD and MNTD) into unique (a-c) and shared fractions (d-g) explained by environmental (ENV), historical (HIS) and spatial (SPA) processes. Adjusted R^2 values in bold are statistically greater than expected based on permutation tests.

Names/fractions	Adjusted R^2	p-value	95% Confidence Intervals of adjusted R^2	
Environment (ENV)	**0.350**	**0.000**	0.237	0.514
Historical (HIS)	**0.452**	**0.000**	0.331	0.649
Spatial (SPA)	**0.596**	**0.000**	0.498	0.760
ENV∩HIS	**0.516**	**0.000**	0.418	0.722
ENV∩SPA	**0.616**	**0.000**	0.558	0.784
HIS∩SPA	**0.647**	**0.000**	0.602	0.807
ENV∩HIS∩SPA	**0.668**	**0.000**	0.635	0.847
Independent fractions:				
a - ENV|(HIS∪SPA)	0.021	0.279	-0.003	0.080
b - HIS|(ENV∪SPA)	0.052	0.159	0.009	0.147
c - SPA|(ENV∪HIS)	**0.152**	**0.012**	0.064	0.284
Shared fractions				
d - (ENV∩HIS)|SPA	-0.001	0.531	-0.052	0.079
e - (HIS∩SPA)|ENV	**0.113**	**0.005**	-0.001	0.278
f - (ENV∩SPA)|HIS	**0.043**	**0.034**	-0.019	0.136
g - ENV∩HIS∩SPA	**0.287**	**0.000**	0.161	0.421
Unexplained variation				
h - 1–(ENV∩HIS∩SPA)	0.332	1.000	0.153	0.365

Note: (∩ intersection; ∪ union; | after controlling for).

Spatial and historical variables accounted for the largest fractions of explained variation in diversity metrics (approximately 60%; Table 3.1 & 3.2; Table B6 in Appendix B). Environment also explained a significant proportion of variation, but it was much smaller than historical and spatial effects, ranging from 18% to 38% (Table 3.1 & 3.2; Table B6 in Appendix B), and it did not explain any variation in MPD (Table B6 in Appendix B). Variation explained by spatially structured environmental gradients (fraction f) was relatively small, and significant only for phylogenetic metrics, particularly PD (6%). For all analysis (except for ATA) the fraction representing shared environmental and historical effects was small and non significant. Lastly, a significant contributor to explaining variation in all cases is the shared fraction representing all predictors simultaneously (fraction g), explaining up to 28% of variation (Table 3.1 & 3.2; Table B6 in Appendix B).

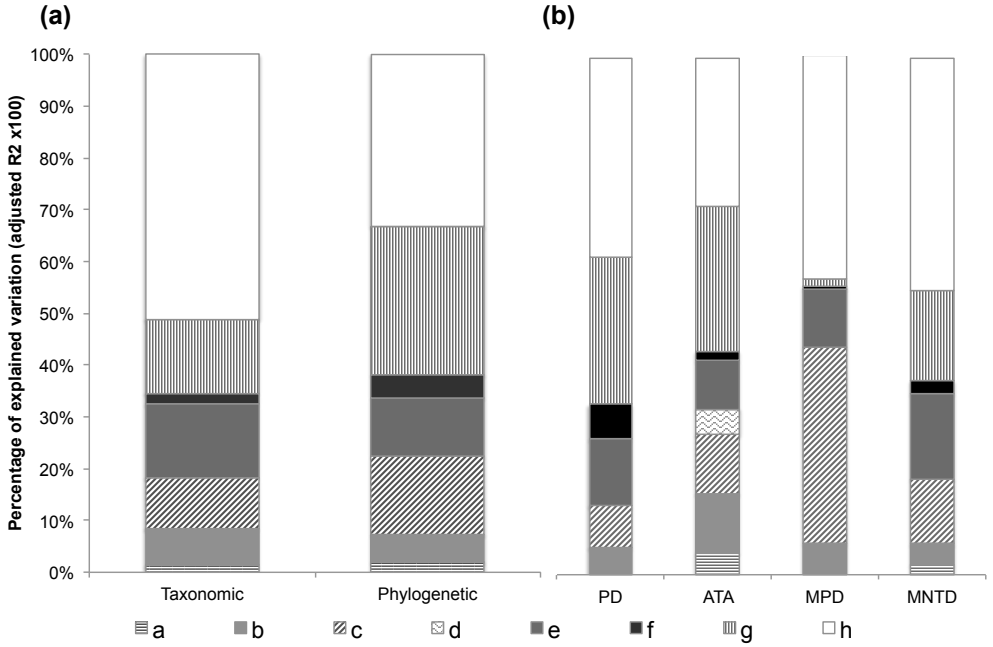

Figure 3.5. Percentage of variation explained (adjusted R^2 x 100) by environmental, historical and spatial predictors represented by fractions of partitioning analysis. (a) Stacked-bar plot partitioning explained variation of taxonomic and phylogenetic community structure. (b) Area graph representing change in variation explained by each fraction associated with different metrics of phylogenetic community structure. Names for reported fractions are as in Figure 2.

Discussion

Our results support the hypothesis of dispersal-based processes being important to taxonomic and phylogenetic structure of neotropical primate communities. Spatial variables explained a larger proportion of variation than did environmental or historical predictors. After performing variation partitioning analysis, the fraction reflecting pure spatial processes (fraction

c) explained the most variation in all independent fractions. Furthermore, all fractions associating spatial variables with historical and environmental predictors (fractions e, f, g) were also large and significant for both diversity metrics. Many community structure studies considering simultaneous effects of ecological and historical processes have used spatial variables or spatial distances as a proxy for historical or regional processes (Kamilar, 2009; Beaudrot & Marshall, 2011; Qian & Ricklefs, 2012), however, their direct role in reflecting said processes remains unclear. Our results show that spatial predictors are good proxies for historical events, but they reflect additional independent variation possibly related to dispersal limitation dynamics.

For any study using spatially distributed data it is important to directly test the influence of spatial autocorrelation (SAC) as it can confound or overestimate effects of predictors analyzed (Legendre, 1993; Dormann *et al*., 2007). Exogenous autocorrelation, which is the result of the spatial dependence of organisms to underlying environmental conditions, which are inherently spatially structured, is the type of SAC that causes problems in statistical analyses. SAC may also be a reflection of endogenous spatial dependence, which is a result of biological processes such as constraints on organism's mobility, dispersal, and conspecific attraction. This type of SAC is related to primate community structure as demonstrated here, and relevant to our understanding of the importance of ecological processes to spatial structure of communities. Endogenous spatial effects can manifest in complex ways, even forming environmental gradients in the absence of significant SAC (Dormann *et al*., 2007). In our study much of the variation explained by environmental and historical components was spatially structured (represented by the relatively large and significant shared fractions). Significant spatial structure was indicated not only by simple associations (fractions d, e and f) but also by more complex spatial interactions (fraction g). Such interactions highlight the importance of investigating complementarity among multiple mechanistic hypotheses (Tello & Stevens, 2010), and testing significance beyond just unique effects (fractions a, b and c) as is usually done.

Our findings support the idea that hypotheses applied to taxonomic community structure can be extended to the phylogenetic component of biodiversity, as the relative contributions of environmental, historical and spatial processes were similar between diversity metrics. However, further examination of phylogenetic metrics suggested a more complex relationship: variation in PD and MNTD were explained mostly by spatial processes, variation in ATA was explained by a combination of all predictors, and MPD was better explained by historical and spatial predictors, with no environmental effects.

Environmental control, historical and spatial processes structuring communities— At large spatial scales encompassing entire regions, as in this study, species distributions are largely determined by processes that affect speciation, extinction and dispersal dynamics (Ricklefs, 1987; Cavender-Bares *et al*., 2009). In our study, most variation of taxonomic and phylogenetic structure in neotropical primate communities was explained uniquely by purely spatially structured variation, which may be related to dispersal limitation of certain clades. For instance, platyrrhine clades are not homogeneously distributed throughout tropical forests and this uneven

distribution is likely related to differences in the location of centers of origin, diversification and dispersal rates among groups (da Silva & Oren, 1996; Rosenberg, *et al*., 2009). Some clades tend to be more dispersal-limited than others, which can generate patterns among clades and certain regions determined by neutral dynamics (Beaudrot & Marshall, 2011). Furthermore, even though primates are known to be highly mobile and able to travel large distances, species are known to restrict their movements to known areas of forest to increase their foraging efficiency and reduce predation risk (Janson & Chapman, 1999). Kamilar & Guidi's (2010) found no phylogenetic structure in neotropical primate communities, consistent with our findings, suggesting that deterministic processes such as environmental filtering and competition play a lesser role in structuring primate communities, particularly when analyzed at a regional scale.

Based on the small amount of variance in taxonomic structure explained by environmental variables, our results suggest ecological flexibility of some species (*i.e*. ability to tolerate a broader set of climatic conditions due to their generalist habits), whereby their presence may be determined principally by dispersal history or presence of barriers (Kamilar, 2009). Moreover, that our study group is represented by endotherms that may be less susceptible to environmental variation is consistent with these results. Qian & Ricklefs (2012) find that global patterns of turnover of mammals and birds, which have larger ecological tolerance ranges than ectothermic vertebrates, are less related to environmental distances than to geographical distances. However, environmental variation could have an indirect effect on primate distribution, as it is variables such as seasonality and precipitation that determine type and amount of resources available for food and shelter influencing inter and intra-species competition (Janson & Chapman, 1999). For our data, communities composed of small-range specialist species such as *Callithrix*, *Saguinus* and *Pithecia* tend to be found in areas where environmental conditions are highly stable throughout the year (Central-western Amazon). In contrast, large-ranged medium- to large-bodied generalist species (*Alouatta*, *Cebus*) are represented in communities with high seasonality, where they are able to cope with variation in temperature and precipitation regimes that in turn affect resource availability and activity patterns (Janson & Chapman, 1999).

Geographic variation in mammal diversification rates has been related to features of the environment such as topographic diversity or available energy (Hawkins *et al*., 2007). The significant fraction of independent variation in ATA explained by environmental variables may reflect such a relationship. Climate may influence net species proliferation rates, enhance speciation through adaptive responses to climatic changes, introduce vicariant barriers as climate zones shift across an area, or promote dispersal as populations track preferred climates (Davies *et al*., 2007; Gillman *et al*., 2009). Furthermore, influence of environmental variables in conservatism of niches of taxa is widely known (Hawkins *et al*., 2007; Stevens, 2011). Although environmental conditions may determine the species that are absent from a region due to physiological tolerances they do not necessarily predict the ones that are present. However, the degree to which ecological processes such as habitat filtering can account for phylogenetic community structure will be largely dependent on the discrepancy between species fundamental

and realized niches and the strength of the phylogenetic signal in species realized niches, which are largely determined by environmental conditions (Cardillo, 2011)

Lastly, historical events explained small fractions of independent variation in both taxonomic and phylogenetic structure, while most of their effects were reflected in the shared fractions between spatial and environmental variables. In the Neotropics, riverine barriers may influence community composition particularly for small, less mobile primate species, such as tamarins and marmosets by directly limiting their dispersal (Ayres & Clutton-Brock, 1992); while large-scale biogeographic changes associated with the uplift of mountain ranges and inherent habitat changes during times of climatic fluctuations may have played a prevailing role in the distribution of larger species such as howlers (Cortes-Ortiz *et al*., 2003). However, the direct influence of these historical events on community composition has rarely been studied. In Primates, such events likely represent productive avenues of future research.

The present study demonstrates importance of analyzing simultaneously multiple mechanisms of assembly of communities to obtain a more comprehensive understanding of current patterns of biodiversity. For neotropical primates, spatial effects, probably linked to differences in species dispersal abilities and history of lineage diversification, were the most important predictors of taxonomic composition. However phylogenetic diversity and structure appeared to be more related to ecological and spatial processes interacting in complex ways. Further research incorporating information such as species abundances, species-specific dispersal rates, habitat heterogeneity, and paleoclimatic information may increase our understanding of primate community assembly. In addition, investigating directly the effects of biotic interactions by examining species co-occurrence (see Kamilar & Ledogar, 2011) will likely provide insightful information regarding the roles of competition, and biotic interactions in the structure of primate communities.

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CHAPTER 4. PRIMATE NICHE OVERLAP AND INFLUENCE OF PHYLOGENETIC NICHE CONSERVATISM ON STRUCTURE OF LOCAL PRIMATE COMMUNITIES[2]

Introduction

The relationship between community structure and phylogenetic similarity remains an important area of research in ecology. At a local level, biotic interactions (*e.g.* competition, facilitation, mutualism) have been attributed to a key role in maintaining community structure (Diamond, 1975; Gotelli & McCabe, 2002). Here, niche differentiation allows highly diverse assemblages to coexist with limited competition (MacArthur, 1958). Evolutionary factors may also influence species coexistence since recently diverged taxa often share many ecological traits and strategies inherited from their common ancestor, leading to similar ecological niches, a tendency termed niche conservatism (Wiens & Graham, 2005). Such a pattern results when closely related species are more ecologically similar than would be expected based on phylogenetic relatedness (Losos, 2008). Further contributing to these patterns is that in local communities organisms do not select habitat independent of type and quality of available resources. Rather, organisms exhibit preferences linked to both intrinsic evolutionary histories that confer particular traits for utilizing said resources, as well as to geological and biogeographic history of habitats they occupy (Morris, 2011, and references therein). Evaluating degree of evolutionary lability or conservatism in species' niches, and testing whether niche conservatism constrains local community composition, is key to understanding roles of ecological and evolutionary processes in community assembly.

Within communities, niche conservatism may be reduced, as the initial ecological similarity that results from common ancestry would likely increase competition leading to competitive exclusion and ensuing ecological differentiation during initial steps of community assembly (colonization phase) (Webb *et al.*, 2002; Lovette & Hochachka, 2006). This process of "erosion" of niche conservatism is most evident in adaptive radiations, where sympatric species have largely diversified with concomitant differentiation in traits related to resource use and habitat partitioning (*i.e.* Cuban anole lizards, Losos *et al*., 2003). In communities composed of closely related species, habitat partitioning is expected to be intrinsically associated with evolutionarily conserved traits, which allow species to exploit resources available and thus maintaining local coexistence. However, few studies have incorporated species evolutionary histories into analyses of niche partitioning (see Losos *et al*., 2003, Sheth *et al*., 2009).

If coexistence is determined principally by processes such as current environmental conditions, resource limitation and/or habitat filtering, then coexisting closely related species may be more ecologically divergent than predicted by their phylogenetic relationships (Losos, 2008; Wiens & Graham, 2005). This would suggest that competitive interactions influence local community assembly. For example fitness costs resulting from overlapping resource needs among coexisting species can lead to recently diverged species segregating by habitat as

[2] In review, *American Journal of Primatology*

evidenced in leaf-warblers (Richman & Price, 1992), oaks (Cavender-Bares *et al.*, 2004), wood-warblers (Lovette & Hochachka, 2006) and ultimately to phylogenetic overdispersion in communities (Bryant *et al.*, 2008; Cooper *et al.*, 2008). In contrast, if coexistence is determined by conservatism of niche characteristics over evolutionary time, then coexisting closely related species are expected to be more ecologically similar than expected based on their phylogenetic relatedness, presenting phylogenetic clustering in local communities (Wiens & Graham, 2005; Losos, 2008). These patterns have been evidenced in rainforest trees (Webb, 2000), emydid turtles (Stephens & Wiens, 2009) and high elevation hummingbird assemblages (Graham *et al.*, 2009).

Neotropical primates are an ideal group for investigating questions regarding mechanisms allowing species coexistence and maintenance of community structure. They represent an adaptive radiation (Norconk *et al.*, 1996), with a large number of sympatric species (up to 14 spp.; Peres, 1993) ranging widely in their time of divergence (>1–32 my.; Fabre *et al*. 2009, Wildman *et al*., 2009), as well as demonstrating wide morphological, dietary and behavioral flexibility (see Kinzey, 1997). Among primate species, competition is reduced through spatial and temporal partitioning of niche space in general (Terborgh, 1983; Peres, 1993), and resource use in particular (Stevenson *et al.*, 2000). Additionally, local environmental variation (*i.e.* seasonality) may alter resource availability and soil nutrient composition, which in turn influences plant nutrient quality, and ultimately resource use (Peres, 1997; Janson & Chapman, 1999). Moreover, evolutionary and historical factors may also influence primate species distribution and community composition (Fleagle & Reed, 1999; Lawes & Eeley, 2000; Kamilar, 2009). For instance, large-scale distribution of primate species is tightly linked to forested areas they inhabit (Haffer, 1997), and presence of rivers, which act as dispersal barriers for many species that promote allopatric speciation (Ayres & Clutton-Brock, 1992). Thus primate community structure is influenced by ecological, environmental and evolutionary processes whose independent and shared influences are important (Gavilanez & Stevens, in press). Studies carried out to understand niche partitioning in primate species only rarely consider influence of evolutionary processes in determining species coexistence (Fleagle *et al.*, 1999; Sheth *et al.*, 2009).

Here we investigate the influence of ecological and evolutionary mechanisms responsible for the maintenance of local community structure in three neotropical primate communities. Initially we assess whether species use habitat preferentially with respect to its availability at each site. We then investigate whether ecological niches, measured by habitat use, are constrained by evolutionary history or rather shaped as a result of species ecological flexibility regarding habitat availability. We quantify species habitat occupancy across a number of local communities, representing different habitat types and species composition. Finally, we test hypotheses regarding influence of evolutionary history on species coexistence in communities, following Losos *et al*. (2003): (H1) If species exhibit niche conservatism (*i.e.* evolutionary history constrains niche space), we expect closely related species (*i.e.* same family) to exhibit less ecological divergence, and higher niche overlap than distantly related species (*i.e.* different

families); (H2) If local coexistence is driven by ecological factors that reduce competition among closely related species, we expect ecological divergence to be higher, and niche overlap to be lower, between closely related species (*i.e.* same family) than between distantly related species (*i.e.* different families). If there were no evidence of any of these processes explaining primate species' local coexistence, we would not find any relationship between ecological divergence and phylogenetic relatedness.

Methods

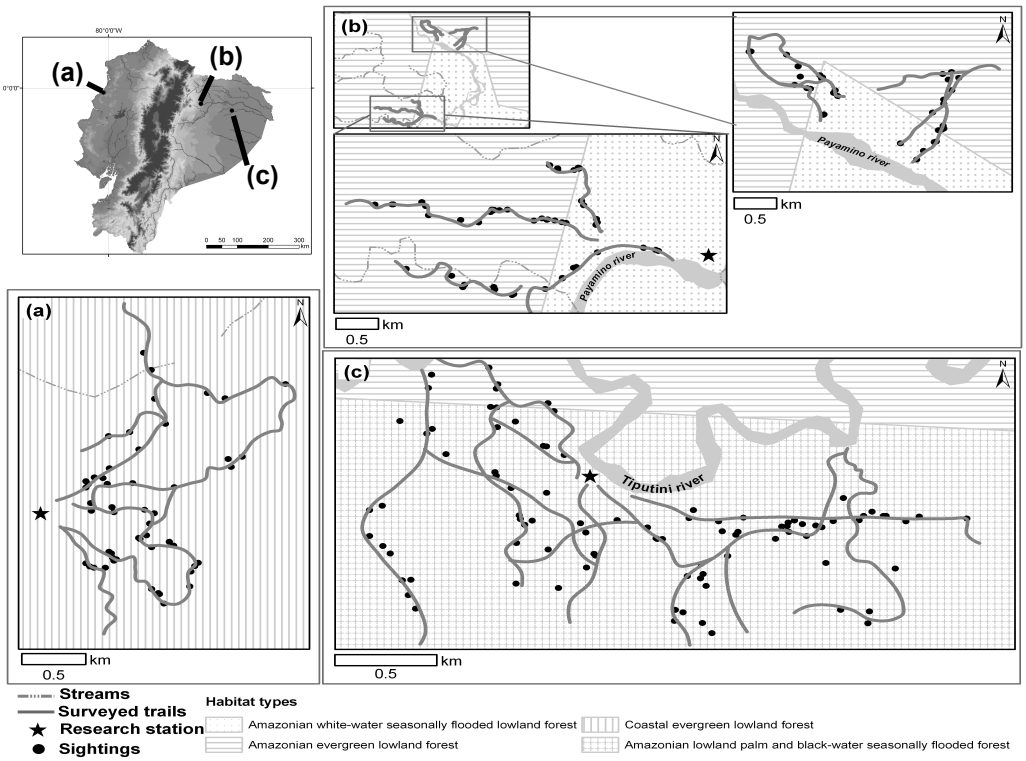

Figure 4.1. Maps of the location of study sites showing surveyed transects and location of sightings (black dots). Stars indicate the location of the research station at each site. Different fill background in maps represents the different forest types present at each site. (a) Jama-Coaque; (b) San Jose de Payamino; (c) Yasuni research station.

Study sites— This study was conducted between May and December 2010 at three sites in Ecuador (Table 4.1; Figure 4.1): (1) Jama Coaque Reserve, located northwest of the province of Manabi near the coast of the Pacific Ocean (0°06.962" S; 80°07.468" W), comprises 333-ha of evergreen lowland coastal and montane forest in the southern-most section of the Choco-Manabi Biological Corridor. Elevation ranges between 250–700 m asl. (2) San Jose de Payamino is a 60,000-ha area of primary evergreen piedmont Amazonian forest situated in the foothills of the Sumaco Volcano, east of the Andes, in the province of Orellana (0°26.975" S; 77°17.936" W). Elevation ranges from 180–460 m asl. (3) Yasuni research station (0°40.453" S; 76°23.846" W) is an evergreen lowland Amazonian forest, located in the province of Orellana, on the right bank

of the Tiputini River. This area comprises 982-ha of relatively undisturbed primary forests, ranging in elevation from 150–290 m asl. It is located within the 1.5-million ha Yasuni Biosphere Reserve.

Table 4.1. Duration of surveys, number, distance of transects and cumulative distances surveyed at the three study sites.

	# Days surveyed	# Transects (length)	Total trail length (km)	Cumulative distance surveyed (km)
Jama	40	5 (1-5km)	12	152
Payamino	40	8 (1-6.5km)	16.5	140
Yasuni	30	9 (1-5km)	15	120

Primate surveys—At all sites we conducted standardized line-transect surveys by two independent observers to determine primate species presence and abundance following guidelines proposed by Peres (1999) and Buckland *et al*. (2010). At each site, transects were walked from approximately 0600 -1200 h and 1400–1730 h at an average speed of 1.25 km/h. During the mid-day inactivity period observers remained relatively quiet at the end of transects to allow sufficient time for animals to redistribute themselves. Transects were visited in a systematic order to assure morning and afternoon surveys began and ended in different locations, and to prevent a single transect from being surveyed more than once every 3 days.

During each encounter we collected the following data: date, time, location on transect, distance from first sighted individual to observer, perpendicular distance from first sighted individual to transect, species, group composition, activity, height in canopy, forest type and phenology of trees where individuals are observed. We marked the location of the tree(s) where primates were observed using a GPS to accurately map distribution of troops across the sampled area. To maximize sampling effort we tracked troops for no longer than 30 minutes during each encounter.

Habitat characterization and use—To characterize habitat availability (availability plots) at each site we conducted habitat surveys in 10x10 m plots placed every 150 m along all transects following methods adapted from Warner (2002). For each availability plot we collected data on habitat type, soil type, proximity to water source, topography, canopy coverage, canopy connectivity, percent epiphytes, phenology, number of dead trees and number of gaps. We also gathered data on structural features of trees (height, DBH, crown shape, crown size, epiphyte cover) to obtain a detailed description of structural and general habitat features of the study sites (see Table C in Appendix C for a description of variables measured and their respective categories).

If a primate sighting was within a 20x20 m radius from the center of an availability plot it was then categorized as an "occupancy plot" for that particular species. Sighting locations were determined by GPS coordinates and flagging tape placed at the moment of the encounter with the group. If sightings were farther away than 20 m from habitat plots, additional occupancy plots

were placed at the location where the sighting occurred to incorporate accurate information regarding species habitat use. All information for habitat characteristics for availability and occupancy plots was collected after primate surveys were completed so as to not influence natural distribution of primate groups as a response to our disturbance during plot set-up.

Data analyses— Randomized *G*-tests of goodness-of-fit were carried out to determine whether species used different habitat features according their availability (Manly *et al.*, 1993). Data were randomized by resampling observations (groups) from a pool based on the expected frequency distribution drawn from availability plots 1000 times to generate a null frequency distribution of *G*-statistics to compare to empirical values. Randomization procedures also help overcome the influence of small sample sizes present in our data set. These analyses were performed in R (R Development Core Team, 2012) using functions in package Vegan (Oksanen *et a*l. 2004).

We calculated a unified measure of niche overlap between species pairs using the method proposed by Geange *et al*. (2011) and R-code provided therein. This method incorporates multiple data types (binary, categorical, percent, count and electivity data), and uses data transformation and density estimation techniques to generate equivalent measures of niche overlap across multiple axes, ranging from 0 (no overlap) to 1 (complete overlap). As tree structural variables are not independent (*i.e.* 5 different measures taken from the same tree) including them all in the calculation of niche space may bias estimates of niche overlap whereby these variables are weighted more heavily than any of the others. We reduced the dimensionality, and multicollinearity of these measures by calculating a composite score for each variable (height, DBH, crown diameter, epiphyte cover) using PCA, and conserving the first derived axis (PCA – 1) as a composite measure for each tree feature (Geange & Stier, 2010). PCA – 1 values were transformed using 1/(X+C), where C is the largest negative value in the PC-scores vector (PCA – 1), plus 1, as proposed by (Rummel, 1970) and then defining this new vector as proportional data in niche overlap analyses (Geange & Stier, 2010). The overlap statistic between species pairs corresponds to the overlapping area between the distributions for each species. Measures of niche overlap derived from different types of data (Table C in Appendix C) were then combined into a single measure of niche overlap by averaging overlap values across different niche axes. We determined whether there was evidence of significant niche differentiation among species pairs (*i.e.* whether the same probability distribution describes the niche of two species) using permutation tests (Gotelli & Graves, 1996; Geange *et al.*, 2011). Species labels were permuted over all species (*i.e.* average niche overlap over all species), which maintains information about total amount of resources used and preserves interspecific variation in resource use. We then calculate pseudo-values of the test statistic that would arise if there were no niche differentiation (no overlap) to generate the null distribution, based on 1000 permutations. The proportion of iterations returning niche overlap values that were lower than observed niche overlap was taken as a '*P*-value' to assess statistical significance in a one tailed test with α 0.05.

Non-metric multidimensional scaling (NMDS), using package vegan (Oksanen *et al.*, 2009) in R, was used to visualize position of species in ecological space, defined by interspecific dissimilarities in habitat occupancy at each site. NMDS is an iterative optimization procedure, which finds the best position of species along *k*-axes so that stress (measure of how distorted distances in original space are in reduced ordination space) is minimized (Legendre & Legendre, 1998; Cox & Cox, 2001). The distance matrix used was the inverse of the matrix of overall niche overlap measures averaged over the dimensions, which represents a measure of association between species pairs.

We tested hypotheses regarding the relationship between phylogenetic relatedness and ecological divergence using a Mantel test (Legendre & Legendre, 1998) using the package ecodist in R (Goslee & Urban, 2007). We used the ecological dissimilarity matrix used in the NMDS procedure described above, and generated a genetic distance matrix using a calibrated phylogeny, with branch lengths (measured as millions of years since divergence, my.) estimated by Fabre *et al*. (2009) using the package ape (Paradis *et al.*, 2004) in R. We then performed an additional randomization procedure described in Sheth *et al*. (2009). This procedure initially tests for linear relationships between distance matrices, but also determines whether pairwise ecological dissimilarity among species pairs from a single monophyletic family are greater than, less than, or no different from pairwise dissimilarities among species pairs from different monophyletic families. This is done by comparing observed pairwise dissimilarity values to the 2.5 and 97.5 percent quantiles of a null distribution of 1000 mean dissimilarity and mean differences. An observed mean dissimilarity lower than the 2.5 percent quantile of the null distribution would lend support to the hypothesis of niche conservatism (H1), while an observed mean dissimilarity higher than the 97.5 percent quantile of the null distribution would lend support to the hypothesis of ecological differentiation to avoid competitive exclusion (H2).

Results

A total of 10 primate species were registered during surveys (Table 4.2). Only one species was present in all 3 communities (*Cebus albifrons*), while all species were shared between Payamino and Yasuni. See Table 4.2 for number of encounters and average troop size for each species at each site.

All species, except for *Callicebus discolor,* showed preferences for particular habitat features (*G*-tests of goodness of fit; Table 4.3). In Jama, capuchins showed preferences for topography (hilltop) and phenology (ripe fruit), while howlers preferred primary forested areas in valleys and hillsides with firm soils, away from water sources, and a highly connected canopy with trees with new leaves. In Payamino, tamarins preferred secondary forests in flat areas with low connectivity close to water sources. Capuchins and squirrel monkeys showed preferences only for primary forests, and red howlers were only found in primary forests. In Yasuni all atelids showed preference for highly connected canopies, but differed in their phenology preferences, with red howlers preferring areas with trees bearing new leaves and spider and wooly monkeys preferring plots with ripe fruit.

Table 4.2. Number of sightings for species observed during surveys along with average group size (range). Last row presents number of availability plots established at each site. Number of occupancy plots for each species equals number of sightings.

Species (family)	Common name	Jama	Payamino	Yasuni
Alouatta palliata (Ate)	Mantled howler monkey	41 7 ind (2-16)		
Alouatta seniculus (Ate)	Red howler monkey		12 5 ind (2-8)	13 6 ind (5-8)
Ateles belzebuth (Ate)	White-bellied spider monkey			13 12 ind (4-25)
Lagothrix lagotricha (Ate)	Brown wooly monkey			15 16 ind (12-24)
Callicebus discolor (Pit)	Red titi monkey		13 4 ind (3-6)	17 4 ind (3-6)
Pithecia monachus (Pit)	Monk saki monkey			15 4 ind (3-5)
Cebus albifrons (Ceb)	White fronted capuchin	15 12 ind (5-16)	23 9 ind (6-12)	14 16 ind (8-30)
Saimiri sciureus (Ceb)	Common squirrel monkey		13 20 ind (16-25)	13 21 ind (10-30)
Saguinus graellsii (Ceb)	Graell's black-mantle tamarin		24 5 ind (3-6)	
Saguinus tripartitus (Ceb)	Golden-mantle saddle-back tamarin			14 6 ind (3-10)
# Availability plots		71	92	91

(Ate: Atelidae; Pit: Pithecidae; Ceb: Cebidae)

Only spider monkeys showed preference for a topographic feature (hillsides). Within cebids, capuchins and squirrel monkeys were only found in primary forests, and capuchins also showed preferences for more open canopies. Tamarins preferred secondary forests in valleys with low canopy connectivity and distant from water sources. Lastly, sakis showed strong preferences for plots with unripe fruit, located on hillsides away from water sources and with high canopy connectivity.

Ecological groups defined by non-metric multidimensional scaling (NMDS) of niche based dissimilarity for all species studied are shown in Figure 4.2. The NMDS configuration was derived from 2 dimensions, with a final stress of 0.1276 indicating a good representation of actual niche dissimilarities. This stress value is much lower than that of a randomized configuration of the data (stress 0.645, $P < 0.05$).

In Jama, overlap between local realized niches of *A. palliata* and *C. capucinus* was high (0.703), although these niches were significantly different based on permutation tests ($P < 0.01$). In Payamino average niche overlap was high (0.671). The species with most dissimilar local realized niches were *A. palliata* and *S. graellsi* (overlap 0.590; $P > 0.001$; Figure 4.2; Table 4.4), while *S. sciureus* and *C. discolor* were the most similar (overlap 0.845; $P = 0.991$; Figure 4.2; Table 4.4).

Table 4.3. Habitat use by each primate species observed at study sites, described by number of plots occupied in relation to number of plots available for each habitat feature (forest type, topography, soil type, proximity to water, canopy connectivity and phenology). Species preferences for particular habitat features (occupancy higher than expected from availability) were based on randomization of goodness of fit tests using Bonferroni adjustments for multiple comparisons.

	Forest Type					**Topography**					**Soil Type**		
	primary	**primary gap**	**secondary**	**secondary gap**	**G-stat P-val**	**base**	**hillside**	**hilltop**	**valley**	**G-stat P-val**	**firm**	**flood plain**	**G-stat P-val**
Jama													
Alouatta palliata (ATE)	29	7	1	4	7.391 *0.031**	4	30	6	1	10.395 *0.015**	25	16	14.287 *0.000***
Cebus albifrons (CEB)	10	2	0	3	2.799 0.451	0	3	12	0	21.995 *0.001***	13	2	0.136 0.745
Jama-availability	37	13	9	12	NA	4	38	19	10	NA	59	12	NA
Payamino													
Alouatta seniculus (ATE)	*12*	0	0	0	14.286 *0.003***	0	*6*	*4*	2	4.794 0.186	11	1	1.111 0.491
Callicebus discolor (PIT)	9	4	0	0	4.692 0.163	5	6	0	2	3.467 0.337	12	1	1.332 0.337
Cebus albifrons (CEB)	19	2	2	0	13.183 *0.004***	3	14	5	1	3.866 0.266	20	3	0.813 0.477
Saguinus graellsi (CEB)	11	0	13	0	36.877 *0.004***	13	6	1	4	14.083 *0.004***	20	4	0.233 0.851
Saimiri sciureus (CEB)	12	1	0	0	11.516 0.014*	4	7	1	1	1.435 0.707	12	1	1.332 0.320
Payamino-availability	42	28	13	9	NA	22	42	16	12	NA	73	19	NA
Yasuni													
Alouatta seniculus (ATE)	12	1	0	0	3.858 0.228	4	6	2	1	2.906 0.358	13	0	0.756 0.630
Ateles belzebuth (ATE)	11	2	0	0	2.219 0.513	5	7	0	1	7.731 *0.049**	11	2	2.449 0.154
Lagothrix lagotricha (ATE)	12	3	0	0	1.921 0.569	4	6	4	1	0.903 0.827	15	0	0.872 0.619
Callicebus discolor (PIT)	13	3	1	0	1.017 0.849	4	7	4	2	3.610 0.258	15	2	1.287 0.232
Pithecia monachus (PIT)	12	3	0	0	1.921 0.557	1	10	3	1	10.071 *0.025**	15	0	0.872 0.642
Cebus albifrons (CEB)	14	0	0	0	*6.885* *0.012**	2	7	5	0	3.299 0.358	14	0	0.814 0.640
Saimiri sciureus (CEB)	13	0	0	0	*6.393* *0.041**	7	3	3	0	4.351 0.213	13	0	0.756 0.606
Saguinus tripartitus (CEB)	4	2	6	2	*36.61* *0.000***	2	9	2	1	8.216 *0.043**	14	0	0.814 0.609
Yasuni-availability	61	21	6	3	NA	26	28	33	4	NA	86	5	NA

* Significant (alpha 0.05), not passing Bonferroni; ** Significant (alpha 0.05), passing Bonferroni

(**Table 4.3.** continued)

	Proximity to water			Canopy Connectivity					Phenology				
	< 20m	> 20m	G-stat P-val	1	2	3	4	G-stat P-val	% young leaves	% flowering	% fruiting ripe	% fruiting unripe	G-stat P-val
Jama													
Alouatta palliata (ATE)	28	13	4.920 *0.048**	1	3	25	12	13.944 *0.004***	24.8	4.4	7.5	6.9	11.729 *0.009***
Cebus albifrons (CEB)	13	2	0.248 0.771	0	4	6	5	2.575 0.454	8.6	20.5	26.4	7.0	19.796 *0.000***
Jama-availability	58	13	NA	5	22	30	14	NA	12.7	9.8	8.6	6.3	NA
Payamino													
Alouatta seniculus (ATE)	12	0	1.463 0.382	0	2	6	4	1.821 0.672	17.8	7.3	14.4	6.7	7.008 0.069
Callicebus discolor (PIT)	10	3	1.992 0.156	0	1	6	6	4.551 0.216	16.7	5.2	7.5	6.3	1.721 0.666
Cebus albifrons (CEB)	18	5	2.805 0.176	1	4	9	9	2.187 0.544	20.0	4.2	7.2	3.9	0.251 0.907
Saguinus graellsi (CEB)	18	6	4.946 *0.042**	13	5	5	1	90.621 *0.000***	14.4	3.8	8.5	2.9	1.969 0.580
Saimiri sciureus (CEB)	11	2	0.710 0.642	0	2	6	5	2.286 0.554	16.0	5.0	7.0	5.0	1.238 0.751
Payamino-availability	82	10	NA	6	25	36	25	NA	17.6	3.2	6.2	4.2	NA
Yasuni													
Alouatta seniculus (ATE)	9	4	0.028 1	0	0	5	8	34.766 *0.000***	24.2	9.2	9.3	6.7	13.036 *0.005***
Ateles belzebuth (ATE)	8	5	0.177 0.759	0	0	5	8	34.766 *0.000***	5.4	11.0	27.2	5.5	16.429 *0.004***
Lagothrix lagotricha (ATE)	13	2	2.617 0.144	0	0	12	3	5.267 0.050	5.7	10.7	24.2	0.0	18.888 *0.002***
Callicebus discolor (PIT)	11	6	0.042 1	0	3	14	0	2.972 0.206	10.2	6.3	8.3	4.6	2.148 0.541
Pithecia monachus (PIT)	14	1	4.696 *0.053**	0	0	11	4	7.148 *0.042**	8.3	11.3	9.3	22.3	58.605 *0.000***
Cebus albifrons (CEB)	10	4	0.123 0.792	2	12	0	0	35.545 *0.000***	12.3	11.8	12.3	5.6	0.471 0.924
Saimiri sciureus (CEB)	8	5	0.177 0.795	0	2	11	0	2.629 0.227	12.5	17.5	21.3	7.5	1.861 0.606
Saguinus tripartitus (CEB)	13	1	4.226 *0.033***	1	8	5	0	9.633 *0.009***	12.3	11.6	10.0	11.2	10.001 *0.050**
Yasuni-availability	61	30	NA	0	22	59	10	NA	8.9	10.0	9.7	3.4	NA

* Significant (alpha 0.05), not passing Bonferroni; ** Significant (alpha 0.05), passing Bonferroni

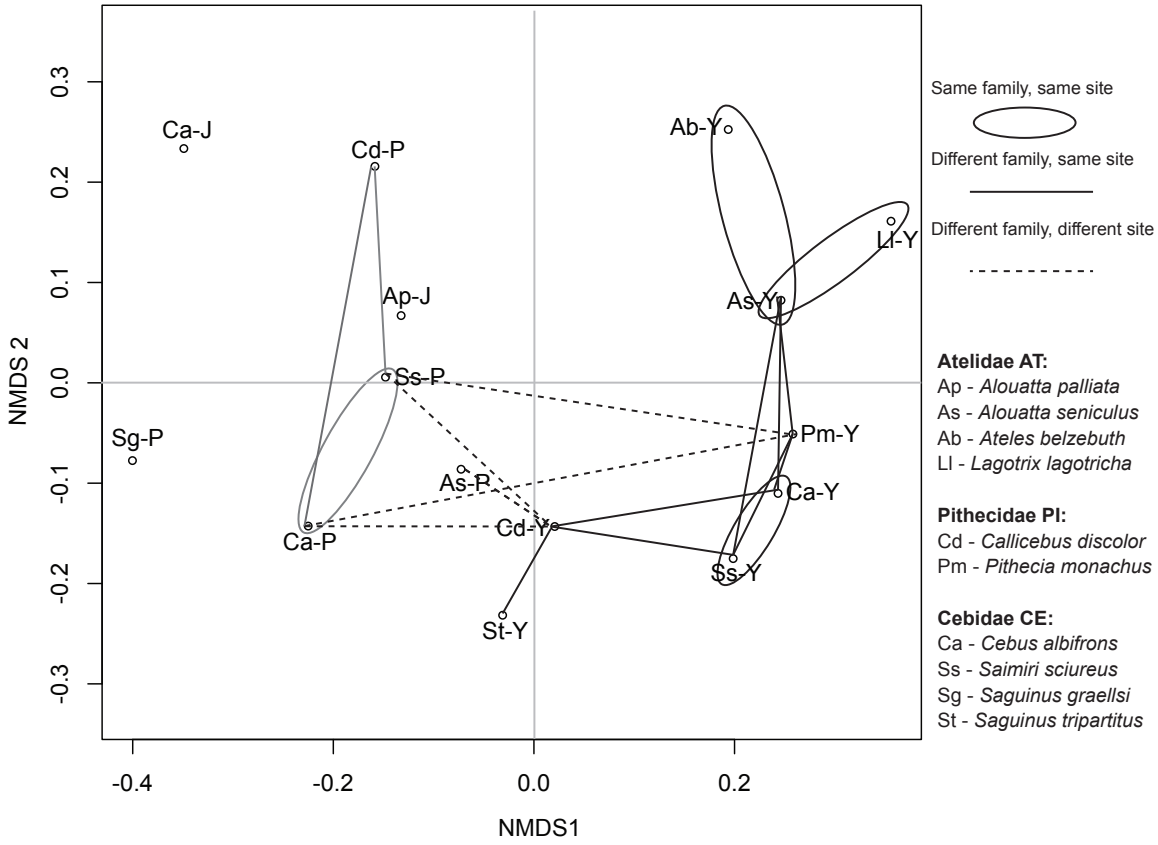

Figure 4.2. Interspecies similarities of unified niche overlap for primate species observed at three forest sites in Ecuador (J-Jama; P-Payamino; Y-Yasuni). Unified niche overlap across all sites was calculated incorporating information on multiple habitat features (see Table C1 in Appendix C). Non-metric multidimensional scaling was used to graphically represent relationships between species pairs based on their level of association (1-niche overlap). Ellipses encircle species pairs from the same family and site, which occupy niches that were not identified as significantly different using null model tests. Lines connect species from different families in the same site (continuous lines) or among sites (dashed lines) for which there were not significant niche differences based on null model tests

Average niche overlap for primate species in Yasuni was 0.680. Here the local realized niches of *S. tripartitus* and two atelids (*A. belzebuth* and *L. lagotricha*) were the most dissimilar (overlap 0.568; P <0.001; Fig 2; Table 4.4). On the other hand, *S. tripartitus* and *C. discolor* had the most similar local realized niches (0.866; P = 0.988; Figure 4.2; Table 4.4). When examining potential niche overlap of species across sites, species with the most significantly different niches were *S. graellsi* from Payamino and four species in Yasuni (*L. lagotricha*, *A. belzebuth*, *A.* seniculus and *P. monachus*; overlap ranges between 0.467 - 0.496, P < 0.001; Fig 2; Table 4.4). The most similar niches were those from *A. seniculus* from Payamino and *C. discolor* from Yasuni (0.732) and *S. sciureus* from Payamino and *C. discolor* from Yasuni (0.714) with their measured niche characteristics not being significantly different based on permutation tests (Fig 4.2; Table 4.4).

Table 4.4. Mean niche overlap (lower triangular matrix) and evolutionary distances (measured as time of divergence in million of years (my.), in the upper triangular matrix) between primate species within and among three study sites in Ecuador. The unified measure of niche overlap (ranging from 0-niches are completely different to 1- niches are identical) was calculated incorporating multiple habitat characteristics, (see Table C1 in Appendix C). Species pairs occupying statistically different niches (based on null model tests) are indicated in bold ($P < 0.05$).

	A1 Alo.pal J	**A2 Alo.sen P**	**A3 Alo.sen Y**	**A4 Ate.bel Y**	**A5 Lag.la Y**	**P1 Cal.dis P**	**P2 Cal.dis Y**	**P3 Pit.mon Y**	**C1 Ceb.alb J**	**C2 Ceb.alb P**	**C3 Ceb.alb Y**	**C4 Sai.sci P**	**C5 Sai.sci Y**	**C6 Sag.gr P**	**C7 Sag.tri Y**
A1.Alo.pal J		6.802	6.802	20.999	20.999	31.828	31.828	31.828	28.701	28.701	28.701	28.701	28.701	28.701	28.701
A2.Alo.sen P	**0.673**		0	20.999	20.999	31.828	31.828	31.828	28.701	28.701	28.701	28.701	28.701	28.701	28.701
A3.Alo.sen Y	**0.606**	**0.577**		20.999	20.999	31.828	31.828	31.828	28.701	28.701	28.701	28.701	28.701	28.701	28.701
A4.Ate.bel Y	**0.605**	**0.583**	0.742		17.168	31.828	31.828	31.828	28.701	28.701	28.701	28.701	28.701	28.701	28.701
A5.Lag.lag Y	**0.557**	**0.547**	0.741	**0.665**		31.828	31.828	31.828	28.701	28.701	28.701	28.701	28.701	28.701	28.701
P1.Cal.dis P	**0.669**	**0.690**	**0.619**	**0.557**	**0.566**		0	28.030	31.828	31.828	31.828	31.828	31.828	31.828	31.828
P2.Cal.dis Y	**0.709**	0.732	**0.642**	**0.587**	**0.619**	**0.643**		28.030	31.828	31.828	31.828	31.828	31.828	31.828	31.828
P3.Pit.mon Y	**0.616**	**0.629**	0.760	**0.598**	**0.700**	**0.594**	**0.713**		31.828	31.828	31.828	31.828	31.828	31.828	31.828
C1.Ceb.alb J	**0.703**	**0.578**	**0.511**	**0.548**	**0.520**	**0.657**	**0.573**	**0.525**		0	0	21.969	21.969	25.536	25.536
C2.Ceb.alb P	**0.766**	**0.742**	**0.591**	**0.558**	**0.543**	0.207	**0.720**	0.577	**0.668**		0	21.969	21.969	25.536	25.536
C3.Ceb.alb Y	**0.598**	**0.667**	0.723	**0.646**	**0.646**	**0.561**	0.702	0.818	**0.508**	**0.577**		21.969	21.969	25.536	25.536
C4.Sai.sci P	**0.722**	**0.736**	**0.633**	**0.627**	**0.545**	0.845	0.714	0.618	**0.627**	0.791	**0.616**		0	25.536	25.536
C5.Sai.sci Y	**0.608**	**0.672**	0.692	**0.625**	**0.625**	**0.572**	0.726	0.764	**0.535**	**0.586**	0.850	**0.623**		25.536	25.536
C6.Sag.gra P	**0.614**	**0.590**	**0.496**	**0.485**	**0.467**	**0.688**	**0.614**	**0.473**	**0.585**	**0.726**	**0.482**	**0.691**	**0.512**		10.982
C7.Sag.tri Y	**0.658**	**0.682**	**0.587**	**0.568**	**0.568**	**0.623**	0.866	**0.655**	**0.557**	**0.685**	**0.646**	**0.667**	**0.665**	**0.610**	

Family: **A1-A5**: Atelidae; **P1-P3**: Pithecidae; **C1-C7**: Cebidae. **Species:** Alo.pal: *Alouatta palliata*; Alo.sen: *Alouatta seniculus*; Ate.bel: *Ateles belzebuth*; Lag.lag: *Lagothrix lagotricha*; Cal.dis: *Callicebus discolor*; Pit.mon: *Pithecia monachus*; Ceb.alb: *Cebus albifrons*; Sai.sci: *Saimiri sciureus*; Sag.gra: *Saguinus graellsi*; Sag.tri: *Saguinus tripartitus*. **Site:** J: Jama; P: Payamino; Y: Yasuni.

All other species pairs, which exhibited high niche overlap (> 0.7), presented significant differences in their realized niches ($P < 0.05$ based on permutation tests). Note that none of these higher and lower overlap values were seen between species belonging to the same family, even when examining niche overlap across sites.

Average phylogenetic relatedness among studied species was 27.54 my (SD 5.53), ranging from 6.8 my between howler species (*A. palliata* and *A. seniculus*), and 31.83 my between pithecids and cebids, and between pithecids and atelids (Table 4). Average ecological dissimilarity (measured as 1-niche overlap) was relatively low (0.365 SD 0.09). The most ecologically similar species belonged to different families (*S. tripartitus*-Cebidae and *C. discolor*-Pithecidae) but were registered at the same site (Yasuni). Conversely, the most ecologically different species were *L. lagotricha* from Yasuni and *S. graellsi* from Payamino. Observed mean difference between pairwise ecological distances among species pairs belonging to a single family and pairwise distances among species pairs in different families were not significantly different from a null distribution of meandifferences (0.005; 2.5% quantile = -0.042, 97.5% quantile = 0.03). Mantel tests indicated no significant correlation between ecological and phylogenetic distances ($rM = -0.1121$, $P = 0.813$).

Discussion

Results suggest local-scale ecological differences, rather than long-term niche conservatism may be operating to promote coexistence within Ecuadorian primate communities. This conclusion is supported by ordination in ecological space (Fig 2), where species are clustering more in terms of sites than phylogeny. Although measures of overlap among species pairs were relatively high, measured ecological niches were still significantly different in many cases, which suggests that axes we selected for characterizing niches were effective for differentiating species in ecological space. Lastly, we did not find a significant relationship between ecological and phylogenetic distance when investigating ecological similarity across sites, indicating little niche conservatism in ecological niche characteristics.

Habitat preferences— Similar to other synecological studies of neotropical primates (Peres, 1997; Stevenson *et al.*, 2000; Haugaasen & Peres, 2005), we documented significant habitat preferences of species at all sites, which may reflect ecological differentiation that promotes coexistence. In general, large bodied species (Atelids) at all sites were found in closed primary forests with high canopy connectivity, while smaller species (Pithecids and Cebids) used primary forests with lower canopy connectivity and in one particular case (*Saguinus graellsi* in Payamino), secondary open forests. This differential use of habitat is likely related to species locomotive behaviors, body size constraints (Youlatos, 2004) and predator avoidance (Terborgh, 1983; Youlatos, 1999). Even in forests with little topographic relief, primates have to navigate several canopy layers as well as deal with habitat perturbations such as gaps and tree-falls that disrupt these layers. This can result in significant impact on primate movements (although impact may vary across taxonomic groups). Canopy connectivity affects arboreal pathways used

by howler and spider monkeys to exploit resources within their territories (Valero & Byrne, 2007; Hopkins, 2011).

Even though all neotropical primates are arboreal, topography has proven to indirectly influence species movement patterns (Youlatos, 2004), as well as social behaviors such as predator avoidance (Cant, 1990) and inter/intra group communication in highly vocal species such as howlers (Whitehead, 1995). Most species showed preferences for high topographic relief, such as hilltops and hillsides/slopes, where tree species diversity is higher and vegetation structure is more complex (Fialho, 2000). Only *Saguinus graellsi* in Payamino preferred flat terrains found in areas where secondary forests, houses, farms and roads were more common. This seemingly idiosyncratic response may be explained by a higher availability of fallen and smaller trees that might provide holes as shelter for this species (de la Torre *et al*., 1995), or feeding resources in smaller secondary trees that cannot sustain weight of larger species. Lastly, observed preferences for primary forests for most species was expected, as these commonly contain the highest tree species richness and abundance of potential food sources compared to secondary forests and gaps (Janson & Chapman, 1999).

All else being equal, habitats are selected so that they yield the highest amount of resources for individuals in a group (Fretwell, 1972). However, in natural systems it is important to take into consideration variables such as nutritional value of available resources, predation risk in areas of high resource availability and inter/intraspecific competition, which may complicate optimal decisions made by consumers (Stephens & Krebs, 1986). In primate communities habitat use is also largely influenced by seasonality and food availability, which can affect resource partitioning, particularly during periods of fruit scarcity (Terborgh, 1983; Peres, 1997; Stevenson *et al.*, 2000). In our study it is clear that differences in plant phenology, that indicate availability of plant resources (new/old leaves, ripe/unripe fruit, flowers), were significant variables determining species habitat selection. This suggests that variation in food availability has important implications for species foraging effort, which may be related to areas and amount of resources needed by individuals to satisfy their daily nutritional requirements (Janson & Chapman, 1999).

Niche overlap— Studies examining niche overlap initially require identifying position of species in the ecological space defined by variables measured, and then determining whether species occupy similar locations in said niche space. Until recently, most studies evaluating niche overlap grouped multiple niche axes based on different types of variables (binary, categorical, electivity) to form a single measure of overlap, without considering intrinsic differences in their distributions. Here we follow methods proposed by Geange *et al* (2011) and account for differences in the distributions of different types of data. This ensures that interpretation of the overlapping density functions is the same for each data type. Most studies of niche overlap in primates have concluded that niche differentiation among coexisting species is strongly associated with variation in behavioral patterns and diet, that allows species to segregate in terms of feeding resources, foraging location, feeding strategies and feeding times

(Stevenson *et al.*, 2000; Haugaasen & Peres, 2005; Sheth *et al.*, 2009). However these are not the only resources species partition, and far less attention has been given to structural composition of habitats in these interact. Such structural composition likely represents significant variables differentiating species niches, and may promote coexistence (see Youlatos, 2004). This is evidenced by our results, which indicate that structural habitat features contribute to significant niche differentiation among species.

We find that within sites, species show high niche overlap, although many niches are significantly different. Cases where niches were not significantly different occurred in the more species rich Amazonian communities where resources are shared between a larger set of species. Species that presented no significant differences in niche attributes had generalist diets (howlers), or were species with large troop size (capuchins, wooly monkeys) which need to travel larger distances to fulfill feeding requirements of larger troops (Kinzey, 1997). A different case where there were no significant differences among species was recorded for species pairs that were registered foraging in polyspecific associations. Capuchins and squirrel monkeys, which are each other's closest relatives within Cebidae, do not present significantly different niches at both sites where they occur. Mixed groups of *Cebus apella* and *Saimiri sciureus* in central Surinam exhibit marked differences in diet and use of forest strata between these two species (Fleagle *et al.*, 1981) which are variables that were not incorporated in this analyses. However, when examining species niches across sites our results point to ecological differentiation promoting primate community structure, as intraspecific niche differences between populations of the same species (*Cebus*, *Saimiri*, *Callicebus*) or closely related species (same genus, different species) compared across sites were significant. Overall, these results highlight a lack of phylogenetic conservatism at the level of the niche measured in this study.

Ecological and phylogenetic relationships— We find a lack no significant relationship between phylogenetic and ecological distance for our studied species, which suggests minimal conservatism at the structural level of the niche for these species. Similarly, Sheth *et al*. (2009) examined primate habitat occupancy and its relationship to phylogeny in a primate community in Amazonian Ecuador and did not find a clear relationship between phylogenetic and ecological distances among species pairs. They suggest that ecological differences among species facilitate their coexistence. Furthermore, these results may reflect the evolutionary history of neotropical primates, which are a result of a single rapid adaptive radiation undergone roughly 20 million years ago (Fabre *et al*., 2009). Because of this process, most species have similar divergence times, but some have remained largely unchanged through that time, while others have undergone considerable adaptive changes (Fleagle & Reed, 1999; 2004). As a result clades of similar age show different amounts of ecological similarity, creating low correlations between ecological and phylogenetic distance.

While phylogenetic conservatism of species' ecological niches has been demonstrated for some clades, many studies show significant rates of niche evolution (Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009). A study examining a relationship between ecological and

phylogenetic similarity in birds, mammals, and butterflies in southern Mexico (Peterson *et al.*, 2008) demonstrated niche conservatism only among sister-species pairs but not at the family level, which implies niche differentiation is occurring at higher taxonomic levels (genera or families). Studies assessing associations between ecological traits and phylogeny for taxa such as anoles (Losos *et al.*, 2003), birds (McCormack *et al*., 2010) and plants (Cavender-Bares *et al.*, 2006) at local scales, have failed to detect a phylogenetic signal in niche structure. These, and our results concur with the notion that ecological traits have low phylogenetic signal (Harvey, 1996). This could be because ecological traits are so strongly affected by multiple biotic (*e.g.* competition) and abiotic filters, that their evolutionary patterns become obscured (Anderson *et al.*, 2004). Furthermore, it is important to consider that results of any phylogenetic study of ecological traits may be spatially scale-dependent (see Vamosi *et al*., 2009). For instance, Silvertown *et al*. (2006) showed that, for plants, beta and gamma niches (habitat and large scale environments, respectively) are affected by phylogenetic conservatism while alpha niches (within-habitat scale) are not.

Our results indicate that closely related species coexisting in local communities are more ecologically similar than distantly related species, supporting an albeit low level of niche conservatism. Species pairs, such as *Cebus*/*Saimiri, Alouatta*/*Ateles, Alouatta*/*Lagothrix, Pithecia*/*Callicebus*, have ecologically similar niches and high overlap. Such a lack of significant niche differences among closely related species may be maintained by processes such as low interspecific competition (Agostini *et al*., 2010) or spatial and temporal partitioning of resources (Stevenson *et al*., 2000). However, when examining species ecological and phylogenetic similarity across communities, evidence of ecological differentiation is stronger, with populations of similar species showing significantly different niches. These differences may be related to changes in strength of inter/intraspecific competition within and among sites (Stevenson *et al*., 2000), along with the evolutionary age of the radiation which may have provided enough time for niche differentiation among populations of the same species to occur, as found for anoles (Losos, 2003) and Old World warblers (Richman & Price, 1992).

Conclusions—Our results evidence that primate species show preferences for structural features of the habitat, which may help in resource partitioning and ultimately promote coexistence. We find that closely-related species coexisting in a community tend to be similar in their structural niche characteristics on an ecological but not an evolutionary scale. This may mean that the realized niche of a species (or at least some of its dimensions) at local spatial scales is not subject to a strong phylogenetic signal. Considering ecological traits in a phylogenetic context represents a powerful tool for investigating the structure of animal communities. Further examination of the relationship between phylogenetic and ecological similarity in plathyrrhine communities across different spatial scales, as well as incorporating measures of other niche dimensions will help increase our understanding of processes responsible for maintaining community structure in this highly diverse tropical taxon.

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CHAPTER 5. CONCLUSIONS

The chapters of this dissertation integrate a broad array of topics related to the fields of macroecology, biogeography, community ecology and phylogenetics to better understand mechanisms responsible for local and large-scale patterns of species co-occurrence and community structure. By analyzing patterns of co-occurrence at multiple spatial scales, my dissertation contributes towards an understanding of the proximate and ultimate mechanisms responsible for community assembly from a regional pool to the maintenance of local biodiversity. Moreover, evaluating the relative influence of ecological, historical and spatial processes allowed deeper and more rigorous insights regarding the mechanistic basis of primate community structure. Lastly, incorporating phylogenetic information proved to be a valuable tool to explore the evolutionary context of species coexistence at local and regional scales.

In Chapter 2, I used a newly developed tool for analyses of species distributions and patterns of association, considering range size and species richness within individual species ranges (diversity fields, Arita *et al.,* 2008). Range-diversity plots describe the relationship between species richness and range size, providing a way to identify species tendency of co-occurrence in relation to the overall distribution of the entire taxon. Using this approach I find that primate species tend to exhibit higher species richness within their range than the mean richness of species across the entire domain. These results translate into a higher tendency of co-occurrence of species that can be related to the highly productive habitats in which most of these species are distributed (Emmons & Feer, 1997). Areas of high productivity are likely to have many available niches for species to partition, and thereby allow them to avoid competitive exclusion (Kay *et al.,* 1997; Lawes & Eeley, 2000). Furthermore, these high patterns of association may also be related to the inherent tropical diversification of this taxon (Schrago, 2007; Rosenberger *et al*., 2009), coupled with lower dispersal ability (Schloss *et al.,* 2012) and the presence of many biogeographic barriers (Ayres & Clutton-Brock, 1992; Lehman & John G Fleagle, 2006). Further insights were gained from the inclusion of phylogenetic information into diversity field analyses. I find that the degree of relatedness of species within their corresponding ranges is highly variable, and shows geographic effects of river barriers and areas of endemism. For instance, species with small ranges and high range-richness values (positive association) exhibited low levels of phylogenetic diversity (low MPD and MNTD), suggesting that these species were co-occurring mostly with close relatives. The distribution of these species could then be tracked back to the geographic location of the range, found in areas of high endemism (Cardoso-daSilva & Oren, 1996) and productivity (Kay *et al*., 1997) in the Amazon basin. Results from null model analyses with a spreading-dye algorithm (Walter Jetz & Carsten Rahbek, 2001) confirmed a strong influence of dispersal limitation in structuring primate species ranges. For most species the empirical distribution of points in the range diversity plot was not significantly different from that of species simulated under a model of range cohesiveness.

However, results of overall association of species (mean range richness) evidenced that observed mean range-richness was lower than expected based on this null model, suggesting other mechanisms exist that place a limit on the number of species co-occurring within a species range.

While investigating patterns of association across species ranges generates information for species-based inferences under biogeographical settings, much is still to be learned regarding mechanisms responsible for variation in actual community composition (*i.e.* the level where species that have been able to colonize from the regional pool interact). In chapter 3 (Gavilanez & Stevens, 2012) I evaluated importance of niche, historical and spatial processes in determining variation in taxonomic and phylogenetic community structure of 74 neotropical primate species. Using variation partitioning analyses (Peres-Neto *et al.,* 2006), I was able to quantify the amount of variation explained independently by each set of predictors, as well as the explained variation that was redundant among hypotheses (shared fractions). Results suggest that purely spatial processes, such as dispersal limitation (Hubbell, 2001; Kamilar, 2009; Beaudrot & Marshall, 2011), play a stronger role in structuring primate communities than environmental variation and historical events. Moreover, even though environmental (niche) and historical processes alone explained little of the variation in community composition, much of their influence was exerted though spatial gradients in environmental conditions. These underlying spatial gradients make shared fractions of variation explained in these analyses large and significant. Environmental correlates have been attributed as playing important roles in explaining patterns of primate species richness (Kay *et al*., 1997; Peres & Janson, 1999); however, their influence in explaining variation in community structure is less clear. Primates are large homeotherms that may not be directly affected by changes in environmental conditions, but rather indirectly through its effects on resource availability and seasonality of an area. Results generally supported the idea that hypotheses that have previously been applied to taxonomic diversity can be extended to phylogenetic diversity. However, differences in relative contributions of historical, environmental and spatial hypotheses regarding different phylogenetic structure metrics suggest the relationship among different aspects of diversity is far more complex.

The scale at which communities are studied affects the detection of relationships between habitat characteristics, patterns of habitat selection, and species composition (Pearman, 2002). Furthermore, species ecological similarities have an underlying evolutionary basis, as closely related species are expected to have similar ecological requirements (Darwin, 1859). In chapter 4 (*in review, American Journal of Primatology*), I investigated how species evolutionary histories determine their ecological roles within and across communities, as well as its influence on niche partitioning. I conducted primate surveys and habitat assessment evaluations in three primate communities in Ecuador using a novel approach to calculating niche overlap among species proposed by Geange *et al*. (2011). This unified metric combines information from multiple types of data, considering differences in their statistical distributions, making it a more accurate descriptor of species ecological similarities. Species niche overlap was relatively high (>0.5) for the structural habitat features analyzed. Within sites I found that closely related species had niches that were not significantly different, while distantly related species (different families)

showed significant niche differences. In contrast, niches of closely related species across sites are significantly different, which was taken as evidence of ecological differentiation promoting coexistence. There was not a significant relationship between ecological and phylogenetic distance when investigating species across sites, which indicated a minimal extent of niche conservatism on the ecological niche axes measured in this study. While phylogenetic niche conservatism has most often been observed in allopatric species that occupy similar niches (despite a period of evolutionary isolation (*e.g.* Peterson *et al.,* 1999; Lovette & Hochachka, 2006; Gómez *et al*., 2010), these findings suggest that ecological differentiation is acting at large spatial scales promoting differences in species niches. However, the lack of significant differences in niches of closely related species within communities suggests that phylogenetic constraints may be stronger drivers of local community structure. Furthermore, the structural characteristics of the niche that was studied here are much more likely to detect patterns related to more subtle ecological differences that likely allow coexisting species to partition ecological resources within habitats, and not fundamental differences in species' selection of habitats.

Taken together, results of my dissertation demonstrate that taking an integrative approach to understanding community structure provides important insights regarding the interaction of multiple processes responsible for the assembly of local communities. Furthermore, the inclusion of the phylogenetic aspect of biodiversity permits the incorporation of valuable evolutionary information contained in phylogenies to make inferences regarding local and regional coexistence among species; which ultimately determine large-scale biodiversity patterns.

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APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Description of calculation steps to generate information required for diversity field analyses

Steps of an *RQ*-mode analysis to obtain information from a PAM on parameters of species diversity fields. Table A1 shows a hypothetical example.

1. Calculate parameters of PAM

   S = number of rows

   N = number of columns

   F = number of total occurrences (ones) in PAM = sum of all species-richness values (column total) = sum of all range size values (row totals)

   $\bar{s}$ = mean species richness (column sums/N)

   $\bar{n}$ = mean range size (row sums/S)

1. Calculate species richness of sites -s_j (column sums) and range size of species -n_i (row sums)
2. Calculate proportional species richness for each site $s_i^* = s_j/S$
3. Calculate proportional range size for each species $n_i^* = n_i/N$ (Y axis of range diversity plot)
4. Calculate proportional fill of the matrix $f^* = F/(S*N)$ (vertical line of range diversity plot)
5. Calculate mean range richness ($\bar{s}_i$) for each species by summing richness values (row totals, s_j) for sites where species i occurs, and dividing this sum by the range size of that species (n_i)
6. Calculate proportional mean range richness - $\bar{s}_i^*$ (X axes in range diversity plot) by dividing mean range richness values by S

Table A.1 Presence–absence matrix (PAM) showing the distribution of 6 hypothetical species across 9 sites to demonstrate the calculations required for diversity field analyses.

Fill 21 ***f**** 0.39		**SITES *N* = 9**									$\bar{n}$ **= 21/6 3.5**	y axis RDplot		x axis RDplot
		si 1	si 2	si 3	si 4	si 5	si 6	si 7	si 8	si 9	n_i (rowsums)	$n_i^* = n_i / N$	$\bar{s}_i$	$\bar{s}_i^* = s_i/N$
SPECIES *S*=6	sp A	1	0	0	1	1	1	0	0	1	5	0.56	12/5 = 2.4	0.27
	sp B	1	1	0	0	1	0	0	1	0	4	0.44	13/4 = 3.25	0.36
	sp C	0	0	1	0	1	0	0	0	0	2	0.22	6/2 = 3	0.33
	sp D	1	0	0	0	0	0	0	1	0	2	0.22	7/2 = 3.5	0.39
	sp E	0	1	0	1	0	0	1	0	0	3	0.33	6/3 = 2	0.22
	sp F	1	0	1	0	1	0	1	1	0	5	0.56	15/5 = 3	0.33
$\bar{s}$**= 21/9 2.3**	s_j (colsums)	4	2	2	2	4	1	2	3	1				
	$s_j^* = s_j/S$	0.7	0.3	0.3	0.3	0.7	0.2	0.3	0.5	0.2				

Examining species diversity fields (for each species)

7. For each species, create a vector of the species richness of all sites overlapped by the range of a given species (Figure A2.a).
8. Create a species richness frequency distribution (Figure A2.b)
9. Calculate the statistical moments of the distribution: mean, variance and skewness for each species
10. Plot the richness values on a map to show spatial variation in species richness (Figure A2.c)

(a)

	mean	variance	skewness
Diversity field sp A = [4,2,4,1,1]	2.4	2.3	0.21
Diversity field sp B = [4,2,4,3]	3.25	0.92	-0.49
Diversity field sp C = [2,4]	3	2	0
Diversity field sp D = [4,3]	3.5	0.5	0
Diversity field sp E = [2,2,2]	2	0	NA
Diversity field sp F = [4,2,4,2,3]	3	1	0

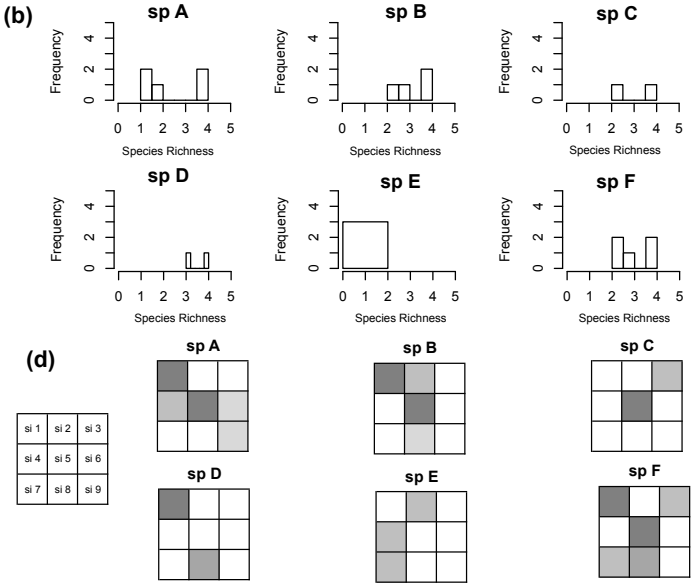

Fig A2. Illustration of (a) statistical parameters of diversity fields (b) species richness frequency distributions and (c) spatial variation in species richness for the hypothetical species used to describe diversity fields. Differences in shading in (c) correspond changes in richness values from s_j table A1

For phylogenetic field analyses of frequency distributions, I computed MPD and MNTD from PAMs derived for each species using the package Picante in R. This generated a vector of MPD and MNTD values for all cells in which the species is present. From the distribution of these values I calculated the same statistical moments as for diversity fields (mean, variance and skewness). Spatial variation in MPD and MNTD values was also represented within the range map of each species (Figure 2.4 second and third columns)

Table A1. Parameters of diversity and phylogenetic fields for 108 neotropical primate species

Species	range size	# overlapping ranges	SR			MPD (my)				MNTD (my)			
			mean	var	skew	sp	mean	var	skew	sp	mean	var	skew
Atelidae													
Alouatta belzebul	643	35	7.11	7.78	0.93	25.70	27.21	1.41	-0.92	6.40	20.38	18.16	-0.50
Alouatta caraya	1184	32	4.77	5.49	1.46	25.71	26.98	8.16	-3.72	7.59	22.19	37.22	-0.89
Alouatta coibensis	12	4	2.50	0.33	0.00	16.06	25.20	2.53	0.00	12.62	18.09	24.16	0.00
Alouatta guariba	441	20	4.24	2.17	0.08	23.49	26.68	16.31	-3.38	5.85	21.07	57.86	-0.77
Alouatta nigerrima	104	38	14.08	6.28	-0.03	25.23	27.29	0.22	-1.20	7.22	12.42	6.39	-0.67
Alouatta palliata	366	17	3.91	3.09	1.13	22.08	23.79	11.24	-1.23	4.47	18.67	32.82	-0.57
Alouatta pigra	123	4	2.33	0.32	1.52	16.33	19.61	7.02	-1.25	13.71	17.80	27.99	-1.08
Alouatta sara	167	22	10.29	11.01	0.75	25.67	26.65	0.53	-0.71	9.91	16.68	11.10	0.00
Alouatta seniculus	1978	82	10.17	20.42	0.08	26.12	27.23	2.18	-2.46	8.01	17.12	22.23	1.09
Ateles belzebuth	585	42	11.63	13.46	0.72	26.72	27.35	0.80	-1.41	10.64	16.23	10.99	0.48
Ateles chamek	758	60	13.13	12.96	0.08	26.24	27.20	0.49	-0.86	8.88	15.44	8.87	0.69
Ateles fusciceps	96	11	5.91	3.11	0.91	21.37	24.71	1.57	-0.32	6.48	15.86	14.52	0.26
Ateles geoffroyi	394	9	2.89	1.22	1.37	20.68	22.73	11.62	-0.66	7.04	20.34	16.88	-1.94
Ateles hybridus	121	19	7.31	5.76	0.64	25.28	25.82	1.91	-1.45	10.90	17.91	12.33	-0.20
Ateles marginatus	332	28	6.81	2.89	1.46	25.73	28.21	0.66	-1.81	6.55	21.19	12.45	-1.43
Ateles paniscus	390	30	8.91	7.53	1.74	26.41	27.55	0.15	1.02	7.03	16.46	6.20	0.59
Brachyteles arachnoides	75	11	5.69	0.79	0.65	23.05	28.11	0.81	-0.98	9.12	22.05	12.53	-0.76
Brachyteles hypoxanthus	68	14	6.28	0.71	-0.13	23.12	27.38	1.04	-0.01	8.54	18.72	18.27	0.13
Lagothrix cana	655	66	13.17	13.07	-0.16	25.99	27.29	0.60	-0.67	8.08	15.37	12.87	1.15
Lagothrix lagotricha	272	38	13.05	12.67	1.46	26.58	27.53	0.15	-2.20	10.33	15.73	8.04	-0.37
Lagothrix lugens	99	26	8.39	7.94	0.86	25.70	25.43	1.79	-0.25	10.57	15.68	11.43	-0.10
Lagothrix poeppigii	290	32	15.06	9.28	0.33	26.33	27.38	0.36	-2.36	11.68	14.42	4.19	0.67
Oreonax flavicauda	16	10	8.13	29.27	0.02	23.84	27.25	1.14	0.01	16.56	19.20	38.25	0.83
Pithecidae													
Cacajao calvus	101	33	16.81	8.44	1.68	26.33	27.54	0.07	-0.64	10.29	13.61	4.40	-0.12
Cacajao melanocephalus	247	37	12.01	11.17	2.00	26.45	27.65	0.11	-0.56	8.87	15.67	0.10	-0.20
Callicebus baptista	13	23	15.71	5.57	-1.19	25.79	27.76	0.11	-1.01	8.69	12.02	1.19	-0.11
Callicebus barbarabrownae	91	11	4.20	1.16	0.17	22.97	27.28	6.41	-0.33	6.50	19.50	64.67	-0.22
Callicebus bernhardi	67	23	12.20	3.75	0.20	24.31	27.80	0.26	-0.22	11.01	16.25	6.10	0.56
Callicebus brunneus	84	26	12.55	5.69	-0.08	25.34	27.61	0.40	-0.18	9.60	15.99	11.94	0.37
Callicebus caligatus	37	34	15.88	8.65	-0.18	26.30	27.63	0.09	-0.74	9.28	13.17	5.13	0.27

(**Table A1.** continued)

Species	range size	# overlapping ranges	SR			MPD (my)				MNTD (my)			
			mean	var	skew	sp	mean	var	skew	sp	mean	var	skew
Callicebus cinerascens	76	25	12.32	6.83	0.14	24.77	27.62	0.37	0.67	9.80	15.58	13.17	0.75
Callicebus coimbrai	9	7	4.67	1.47	-0.05	22.66	26.92	3.13	0.51	9.79	16.14	56.25	0.30
Callicebus discolor	108	23	10.91	7.07	-0.93	25.93	27.64	0.47	-1.68	11.87	16.31	11.75	2,52
Callicebus donacophilus	182	17	7.89	5.97	1.58	25.45	27.43	0.53	0.04	11.32	19.96	17.19	-0.35
Callicebus dubius	100	22	14.56	2.45	-0.83	24.68	27.00	0.28	-0.09	9.07	14.24	2.28	0.61
Callicebus hoffmannsi	54	30	14.32	6.80	-0.52	25.55	27.41	0.15	0.03	7.22	11.98	7.76	1.01
Callicebus lucifer	99	33	15.92	14.48	1.01	26.44	27.64	0.04	0.00	9.85	14.30	7.77	-0.05
Callicebus lugens	349	25	9.50	8.10	-0.49	26.15	27.87	1.07	1.13	11.20	18.27	19.49	0.84
Callicebus medemi	26	20	14.83	3.97	-0.34	25.98	27.44	0.09	-0.89	13.84	15.01	2.74	0.30
Callicebus melanochir	26	8	7.85	8.19	1.00	23.58	27.39	1.00	-0.63	10.23	20.69	21.32	-0.48
Callicebus modestus	4	10	10.00	0.00	NA	24.79	27.44	0.00	0.00	15.64	16.06	0.74	0.00
Callicebus moloch	375	30	8.72	6.35	1.30	25.84	27.85	0.37	-0.48	6.80	19.86	18.12	-1.05
Callicebus nigrifrons	205	14	5.11	0.87	0.30	23.03	28.09	1.94	-0.16	4.52	21.71	30.48	-0.04
Callicebus oenanthe	4	9	13.67	3.07	-0.18	24.22	27.18	0.08	0.82	14.54	14.44	0.66	0.02
Callicebus ornatus	14	15	8.67	0.67	0.63	24.16	26.29	0.14	0.43	13.25	16.37	5.98	0.40
Callicebus pallescens	180	6	3.67	1.68	0.76	23.73	29.88	1.52	0.21	20.81	27.44	11.70	-7.27
Callicebus personatus	77	14	6.11	0.87	-0.51	23.10	27.38	1.47	0.17	8.33	17.65	27.96	0.33
Callicebus purinus	73	29	16.83	11.25	1.39	26.66	27.81	0.04	0.32	10.62	13.64	3.30	-0.21
Callicebus regulus	104	25	16.51	9.37	1.80	26.09	27.62	0.10	-0.10	11.12	13.59	2.96	-0.83
Callicebus stephennashi	24	21	15.64	4.25	-0.49	25.84	27.65	0.06	-0.78	10.66	13.64	2.58	0.36
Callicebus torquatus	123	35	13.46	16.52	1.16	26.39	27.74	0.05	-0.14	8.60	14.24	10.44	0.67
Pithecia aequatorialis	56	22	14.88	4.90	1.12	25.90	27.54	0.05	-0.87	11.76	15.12	2.58	-1.03
Pithecia albicans	49	29	17.90	11.29	1.38	26.66	27.79	0.05	0.40	10.62	12.88	2.70	0.45
Pithecia irrorata	532	64	13.67	10.90	0.09	25.92	27.39	0.40	0.01	7.91	15.08	11.49	0.96
Pithecia monachus	416	38	14.43	9.70	0.28	26.50	27.43	0.23	-0.75	10.53	15.06	5.20	0.62
Pithecia pithecia	435	39	9.06	10.56	1.49	25.75	27.66	0.39	2.55	6.35	16.79	11.54	1.22
Chiropotes chiropotes	491	33	9.39	7.58	1.34	26.30	27.73	0.55	1.57	7.08	16.71	12.16	1.08
Chiropotes satanas	113	12	7.00	1.95	1.30	24.67	26.78	1.28	0.37	12.94	19.87	7.10	1.43
Chiropotes utahickae	158	19	8.82	2.04	1.05	25.51	28.14	0.25	-0.12	8.77	20.14	6.54	-0.12
Cebidae													
Callimico goeldii	261	33	14.26	5.28	-1.03	26.36	27.06	0.34	-0.18	10.84	15.35	4.41	1.16
Leontopithecus caissara	2	4	4.50	0.50	0.00	22.30	29.30	0.38	0.00	27.90	26.44	4.26	0.00
Leontopithecus chrysomelas	34	9	5.83	0.97	0.33	22.79	26.69	2.38	-0.06	9.89	19.13	28.77	-0.29
Leontopithecus rosalia	15	8	5.57	0.29	-0.29	24.03	28.32	0.29	-0.09	14.75	21.92	11.99	-0.52
Callithrix acariensis	16	16	13.88	4.13	0.18	24.85	27.11	0.09	0.12	11.46	13.65	2.74	0.62

(**Table A1.** continued)

Species	range size	# overlapping ranges	SR			MPD (my)				MNTD (my)			
			mean	var	skew	sp	mean	var	skew	sp	mean	var	skew
Callithrix argentata	68	23	10.41	8.10	0.75	26.09	27.76	0.26	-0.33	7.36	18.15	23.41	-0.63
Callithrix aurita	82	14	5.89	0.77	0.54	23.05	27.48	1.56	-0.47	4.92	19.78	25.63	-0.47
Callithrix chrysoleuca	27	21	14.30	4.90	0.25	24.66	27.26	0.17	0.28	10.98	13.62	1.95	1.09
Callithrix emiliae	121	23	9.13	6.46	1.04	25.98	27.59	0.25	-0.17	8.30	19.59	12.00	-0.22
Callithrix flaviceps	23	8	6.08	0.44	-0.09	22.40	27.07	0.37	-3.55	14.85	18.59	1.15	-0.43
Callithrix geoffroyi	81	13	6.14	0.98	-0.50	23.04	27.04	1.71	0.49	7.32	17.05	27.21	0.57
Callithrix humeralifer	44	25	13.94	6.06	-0.53	25.56	27.33	0.16	0.24	6.69	11.75	9.24	1.23
Callithrix humilis	7	16	15.33	2.33	0.38	25.18	26.96	0.03	0.16	12.12	13.28	1.35	0.63
Callithrix intermedia	33	16	11.56	2.53	0.34	24.85	27.62	0.26	0.10	11.46	16.08	4.40	-0.08
Callithrix jacchus	297	9	3.35	1.37	0.55	22.95	25.71	3.87	-0.31	6.28	21.33	41.09	-0.72
Callithrix kuhlii	22	8	6.13	0.98	-0.25	23.58	26.73	1.83	-0.14	10.23	17.67	28.08	0.27
Callithrix leucippe	7	13	12.20	14.70	-0.41	24.91	27.03	0.02	0.41	9.56	13.26	32.09	0.41
Callithrix mauesi	13	18	12.33	7.47	0.84	25.86	27.34	0.21	-0.23	11.33	13.33	6.42	-0.72
Callithrix nigriceps	21	16	12.78	1.69	-0.29	25.48	27.53	0.07	0.01	13.23	15.29	0.66	0.36
Callithrix penicillata	627	23	4.21	1.61	1.05	25.41	26.73	4.16	-0.57	7.71	21.54	37.53	-0.55
Callithrix pygmaea	580	44	14.81	7.00	0.89	26.70	27.35	0.26	-0.61	10.31	14.70	3.76	0.25
Callithrix saterei	15	18	14.38	7.98	-0.25	25.02	27.38	0.24	-0.14	10.91	13.01	5.94	-0.77
Saguinus bicolor	7	18	17.00	18.00	0.00	26.34	27.41	0.02	0.00	10.02	10.67	4.84	0.00
Saguinus fuscicollis	683	49	14.29	8.04	0.34	26.66	27.25	0.40	-1.09	10.14	14.91	4.28	0.35
Saguinus geoffroyi	38	7	5.78	0.42	0.21	20.18	25.77	0.58	0.59	7.89	18.59	11.94	0.18
Saguinus graellsi	106	23	14.13	4.96	0.82	25.93	27.17	0.65	-2.69	11.87	14.52	4.20	-1.26
Saguinus imperator	128	22	15.02	2.10	0.72	25.98	26.85	0.19	-0.20	10.46	14.75	1.74	-0.43
Saguinus inustus	153	29	12.12	11.47	2.34	26.56	27.67	0.07	-0.82	9.72	16.18	9.44	-0.25
Saguinus labiatus	154	50	15.85	8.06	1.69	26.45	27.26	0.31	-0.69	9.20	13.36	2.92	-0.14
Saguinus leucopus	35	8	6.31	2.10	-0.16	20.94	25.93	0.67	-0.15	12.39	19.02	19.45	0.00
Saguinus martinsi	18	16	12.38	14.84	0.48	25.50	27.18	0.02	1.14	10.82	12.36	2.84	-0.41
Saguinus midas	433	28	8.98	6.92	1.67	26.12	27.51	0.18	0.25	6.54	16.60	6.98	0.55
Saguinus mystax	232	37	16.19	6.79	1.46	26.62	27.55	0.09	-0.18	10.80	13.72	3.05	-0.31
Saguinus niger	162	19	8.40	2.88	0.76	25.38	27.63	0.94	-0.32	8.54	20.43	7.49	0.02
Saguinus oedipus	42	11	6.59	1.13	-0.08	21.37	25.15	0.34	1.25	6.48	16.10	7.19	0.88
Saguinus tripartitus	27	19	15.27	2.02	0.59	25.93	27.47	0.02	0.14	13.82	15.45	0.56	0.01
Cebus albifrons	1392	84	11.69	18.16	-0.32	26.02	26.96	2.23	-3.22	8.08	15.70	14.35	1.20
Cebus apella	2041	83	9.01	8.49	0.25	26.15	27.33	1.96	-5.92	8.08	17.36	12.57	-0.56
Cebus capucinus	197	12	4.23	1.95	1.27	21.16	25.53	1.56	-1.43	5.70	20.06	20.18	-0.93
Cebus kaapori	72	11	7.17	1.73	1.91	25.04	26.28	0.60	-0.12	13.67	18.63	1.22	-1.36

(**Table A1.** continued)

Species	range size	# overlapping ranges	SR			MPD (my)				MNTD (my)			
			mean	var	skew	sp	mean	var	skew	sp	mean	var	skew
Cebus libidinosus	1508	46	5.29	11.68	1.77	26.30	26.77	3.93	-0.93	8.18	21.82	33.03	-0.82
Cebus nigritus	425	18	4.34	3.01	-0.05	23.11	27.03	6.76	-1.59	4.97	20.92	54.17	-0.64
Cebus olivaceus	657	27	6.84	9.65	0.08	26.24	27.50	3.83	-2.77	8.85	19.39	32.08	0.48
Cebus xanthosternos	175	14	4.32	1.64	2.17	23.48	26.91	5.18	-0.11	5.82	19.67	54.82	-0.23
Saimiri boliviensis	677	46	12.20	20.02	-0.16	26.63	27.03	1.09	-2.54	10.11	16.41	15.98	1.12
Saimiri oerstedii	12	4	10.29	11.69	1.26	19.72	27.45	0.64	-1.91	21.48	16.96	10.83	0.21
Saimiri sciureus	1098	56	4.40	0.30	0.41	25.50	26.28	0.00	-0.41	7.37	21.66	0.06	0.41
Saimiri ustus	618	56	10.24	15.69	0.36	25.50	27.38	0.80	-1.57	7.37	17.86	23.16	-0.06
Saimiri vanzolinii	5	23	18.00	12.57	0.00	26.37	27.82	0.02	0.56	10.15	11.23	0.94	-0.23

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Selection criteria for communities to be included in analyses

Several criteria were used to select sites to be included in analyses, particularly to control for differences in sampling effort, census techniques and methods of data collection.

1. Data had to have been based on real sightings. Records of presence based on acoustic cues and indirect records were not included.
2. Studies that carried out surveys for less than 21 days were excluded since they may fail to account for the presence of rare or less abundant species (Peres, 1999).
3. Surveys that were carried out along linear transects of over 10 km were preferred, as they are carried out in accordance with the standardized procedures of primate sampling (Brockleman & Ali, 1987; Peres, 1999). However, studies that were carried out for the minimum required time along rivers or non-linear transects because of geographical or logistical limitations, but covered a wide range of habitats present in the sampled area were also included.
4. To take into account sampling effort in terms of area, the area sampled must have included most of the habitat types present, and it had to cover at least 5% of the total area where the study was carried out.

Some of the studies incorporated into the analyses come from long term data in primate composition, without actually representing a census, but represented locations where community composition had been assessed adequately by long term studies.

Communities were considered as unique if they complied with the following criteria: were separated by at least 50km from other localities, or if they were closer but separated by a major river (which are considered to be important barriers for the distribution of some neotropical primates; Ayres & Clutton-Brock, 1992; Peres et al., 1996). They were also considered independent communities if they were found in different adjacent ecoregions, as habitat is considered to be an important determinant in the composition for primate communities because of its influence on the type and abundance of resources (Janson & Chapman, 1999).

The determination of individual communities was carried out by entering the geographic coordinates of the localities in ArcMap 9.1 (ESRI) along with a layer of the WWF ecoregions (Olson *et al*., 2001) and one representing major river systems for America. After the shapefile of the localities was introduced, a buffer of 50km was drawn around each individual locality, and if these were overlapping, then just one of the overlapping localities was randomly selected.

After considering these criteria, 74 of 110 potential localities were included in the analyses. However, it is important to point out that there are regions in central-eastern and north-eastern Amazonia, and particularly the Atlantic forests, that were not represented in this study, due to a paucity of studies that conform to our somewhat conservative selection criteria.

Owl monkeys (*Aotus* spp.) were not included in any of the analyses due to their nocturnal habits that make these species difficult to observe, and thus records of their presence are not common.

Procedure used to assign communities to river basins and pleistocene refugia

To include riverine barriers as predictor variables communities were assigned to a river basin, limited by potential river barriers. These potential river barriers were selected based on an overlay of layers of location of communities, major rivers of South America and polygons of primate species range maps (Nature-Serve, Patterson *et al*., 2005). We selected rivers that

represented limits to the distribution of at least a pair of congeneric species. Based on this criterion 15 major rivers were considered riverine barriers. We then generated a matrix of dummy variables for the 15 river basins that assigned communities to a particular basin. All communities west and north of the Andes and Central America were placed in a single trans-Andes category (Figure 1; Table S1). A similar procedure was followed to assign communities to proposed Pleistocene refugia [following Prance (1982)] to generate a predictor matrix of dummy variables for this hypothesis. Each community was assigned to the geographic center of the closest proposed Pleistocene refuge. Communities were assigned to one of 26 proposed refugia (Figure 1; Table S2).

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Table B1. List of sites used in analyses and their respective primate richness

Site**	Country	Latitude[a]	Longitude[a]	Species Richness
1. Agua Limpa	Brasil	-15.933	-47.900	3
2. Altamira	Brasil	-6.583	-68.900	10
3. Ampiyacu	Peru	-3.167	-71.833	3
4. Apoteri	Guyana	4.017	-58.567	8
5. Arroyo Chuchi	Bolivia	-15.583	-62.750	4
6. Barro Colorado Island	Panama	9.167	-79.850	3
7. Barro Vermelho I	Brasil	-6.451	-68.760	12
8. Barro Vermelho II	Brasil	-6.472	-68.767	7
9. Berbice	Guyana	6.450	-57.667	6
10. Bocas del Toro	Panama	9.417	-82.333	2
11. BP Los Cedros	Ecuador	0.309	-78.779	3
12. Caparu	Colombia	-1.099	-69.502	7
13. Cobija	Bolivia	-11.167	-68.967	6
14. Cocha Cashu	Peru	-11.833	-71.383	12
15. Condor	Brasil	-6.741	-70.786	10
16. Corcovado National Park	Costa Rica	8.550	-83.583	4
17. Curaray North	Bolivia	-2.033	-74.883	5
18. Curaray South	Bolivia	-2.167	-74.650	4
19. Cuyabeno Wildife Reserve	Ecuador	0.283	-75.867	8
20. Darien	Panama	7.800	-77.667	4
21. Caratinga Biological Station	Brasil	-19.833	-41.833	4
22. El Triunfo	Bolivia	-15.250	-64.250	4
23. El Tuparro National Park	Colombia	5.283	-68.367	3
24. Espiritu Santo	Brasil	-19.200	-40.117	4
25. Fazenda Exp. Catuaba	Brasil	-10.067	-67.600	8
26. Fazenda Mariana	Brasil	-11.409	-61.568	9
27. Fazenda Sao Jose	Brasil	-22.367	-47.467	3
28. Fortuna	Brasil	-5.134	-67.238	13
29. Hato Masaguaral	Venezuela	8.567	-67.583	2
30. Igarape Jaraqui	Brasil	-4.350	-66.517	10
31. Itatiayia	Brasil	-22.417	-44.583	4
32. Ixiamas	Bolivia	-13.667	-68.167	3
33. Kayapo C. E. S	Brasil	-7.688	-51.874	4
34. La Chonta	Bolivia	-16.607	-62.783	4
35. La Suerte	Costa Rica	10.442	-83.771	3
36. Lago da Fortuna	Brasil	-5.159	-67.239	6
37. Lago Uaucazu	Brasil	-4.333	-62.467	12
38. Machalilla National Park	Ecuador	-1.567	-80.717	2
39. Maraca Island	Brasil	3.417	-61.550	5
40. Mbaracayu	Paraguay	-23.817	-56.133	2
41. Noel Kempff Mercado	Bolivia	-13.600	-60.917	5
42. Nova Empresa	Brasil	-6.800	-70.733	5
43. Pajaral	Bolivia	-14.950	-63.517	6
44. Calakmul	Mexico	17.483	-92.050	2
45. Pando	Bolivia	-12.388	-68.586	10
46. Panguana	Peru	-9.583	-74.950	4
47. Paracou	Guyana	5.301	-52.924	6
48. Paranabiacaba	Brasil	-24.333	-48.250	3
49. Perserverancia	Bolivia	-14.633	-62.617	5

** Numbers correspond to those on maps/tables; [a] Units-Decimal Degrees

(**Table B1.** continued)

Site**	Country	Latitude[a]	Longitude[a]	Species Richness
50. Pico da Neblina	Brasil	0.393	-65.150	4
51. Yasuni National Park	Ecuador	-0.700	-75.467	9
52. Porongaba	Brasil	-8.667	-72.783	11
53. Potaro Plateau	French Guyana	4.983	-59.583	6
54. Punta Leona	Costa Rica	9.693	-84.661	2
55. Rio Cuyuni Basin	Venezuela	6.716	-61.608	3
56. Rio Jau	Brasil	-1.836	-61.586	10
57. Rio Tapajos	Brasil	-2.567	-54.967	8
58. Sacado	Brasil	-6.759	-70.786	4
59. Samiria	Peru	-5.017	-73.983	7
60. San Jose	Bolivia	-17.833	-60.833	3
61. San Luis	Bolivia	-14.717	-63.967	3
62. Serra dos Orgaos	Brasil	-22.458	-45.995	4
63. Station des Nouragues	French Guyana	4.083	-52.667	6
64. Tapiche River	Peru	-5.655	-74.004	9
65. Tikal	Guatemala	17.250	-89.583	2
66. Tinigua National Park	Colombia	2.667	-74.167	6
67. Tiputini Biodiversity Station	Ecuador	-0.618	-76.171	9
68. Trinity Hills Wildlife Reserve	Trinidad	10.133	-61.133	2
69. Tropenbos	Guyana	5.011	-58.600	8
70. Upper Nanay	Peru	-3.450	-74.533	6
71. Upper Urucu River	Brasil	-4.833	-65.267	12
72. Vira Volta	Brasil	-3.283	-66.233	12
73. Von Humboldt	Peru	-8.750	-75.083	3
74. Xixuau Nature Reserve	Brasil	-0.800	-61.550	7

** Numbers correspond to those on maps/tables; [a] Units-Decimal Degrees

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Table B2. Description of communities assigned to one of 15 river basins.

Map River Basin names	# communities assigned	Communities reference numbers**
Rio Negro - Magdalena - Orinoco	3	23, 29, 66
Orinoco - Amazonas - Atlantic	9	4, 9, 39, 47, 53, 55, 63, 68, 69
Orinoco - Rio Negro	2	50, 74
Rio Negro - Japura - Amazonas	3	12, 19, 56
Japura - Maranon	6	3, 17, 18, 51, 67, 70
Maranon - Ucayali	3	46, 59, 73
Ucayali - Purus - Amazonas	14	2, 7, 8, 15, 28, 30, 36, 37, 42, 52, 58, 64, 71, 72
Purus - Madeira	5	13, 14, 25, 32, 45
Tapajos - Amazonas	1	57
Madeira - Xinju - Paraguay	9	5, 22, 26, 34, 41, 43, 49, 60, 61
Xinju - Tocantins	1	33
Tocantins - San Francisco	1	1
Parana - Paraguay	1	40
San Francisco - Parana - South Atlantic	6	21, 24, 27, 31, 48, 62
Trans-Andes	10	6, 20, 11, 16, 20, 35, 38, 44, 54, 65

* See Figure 1 for map of location of major rivers.
** See Table B1 for references to community numbers.

Table B3. Description of communities assigned to 20 Pleistocene refugia.

Map Refuge names*	# communities assigned	Communities reference numbers***
A. Panama-Darien	8	6, 10, 16, 20, 35, 44, 54, 65
B. Choco	2	11, 38
C. Imeri	2	23, 50
D. Napo	19	2, 3, 7, 8, 12, 15, 17, 18, 19, 28, 36, 42, 51, 58, 59, 64, 67, 70, 73
E. Tefe	3	37, 71, 72
F. Sao Paulo de Olivenca	1	30
G. Peru - Acre	7	13, 14, 25, 32, 45, 46, 52
H. Beni	9	5, 22, 34, 40, 41, 43, 49, 60, 61
I. Rio Espirito Santo	5	21, 27, 31, 48, 62
J. Bahia	1	24
K. Araguaia	1	1
L. Apuana	1	26
M. Tapajos	1	33
N. Manaus	2	56, 74
O. Trombetas	1	57
P. E. Guyana	2	47, 63
Q. W. Guyana	4	4, 9, 53, 69
R. Imataca	2	39, 55
S. Paria	1	68
T. Rancho Grande	2	29, 66

* See Figure 1 for map of location of Refugia.
** Taken from Prance (1982).
*** See Table B1 for reference numbers of communities.

Table B4. Summary statistics and Pearson correlation coefficients between ecological variables used in the analyses.

	Mean	Min	Max	Median
Net Primary Productivity (gr C km^2-1)	8.36E+11	6.39E+10	1.11E+12	9.575E+11
Min. Temperature (°C)	20.1	12.8	23.5	20.5
Max. Temperature (°C)	30.3	23.8	33.2	30.8
Annual Mean Temperature (°C)	25.2	18.8	28.3	25.8
Temperature Seasonality	89.9	25.9	313.0	57.2
Min. Precipitation (mm^3)	72.0	2.0	200.0	61.0
Max. Precipitation (mm^3)	317.7	97.0	749.0	310.0
Annual Precipitation (mm^3)	2239.6	384.0	4319.0	2379.5
Precipitation Seasonality	49.5	7.8	101.0	49.2

	NPP	Min Temp	Max Temp	Ann Temp	Temp Season	Min Prec	Max Prec	Ann Prec	Pre. Sea
NPP	-	0.073	0.24	0.15	0.05	0.23	0.25	0.058	0.3
Min Temperature		-	0.79	0.86	0.64	0.42	0.26	0.42	0.44
Max Temperature			-	0.83	0.46	0.22	0.16	0.24	0.25
Annual Temperature				-	0.59	0.35	0.23	0.36	0.38
Temperature Seasonality					-	0.43	0.35	0.55	0.4
Min Precipitation						-	0.23	0.66	0.8
Max Precipitation							-	0.84	0.094
Annual Precipitation								-	0.56
Precipitation Seasonality									-

Table B5. Primate species occurring in the selected communities, along with their numbers of occurrences.

Species	Incidence
Atelidae	
Brachyteles hypoxanthus	1
Lagothrix poeppigii	1
Alouatta belzebul	2
Alouatta pigra	2
Ateles fusciceps	2
Ateles marginatus	2
Brachyteles arachnoides	3
Alouatta caraya	5
Alouatta guariba	5
Ateles belzebuth	5
Ateles geoffroyi	5
Alouatta palliata	7
Lagothrix cana	8
Lagothrix lagotricha	9
Ateles chamek	12
Ateles paniscus	12
Alouatta seniculus	44
Pithecidae	
Callicebus brunneus	1
Callicebus personatus	1
Pithecia aequatorialis	1
Callicebus nigrifrons	2
Pithecia albicans	2
Cacajao melanocephalus	3
Cacajao calvus	4
Callimico goeldii	4
Callicebus moloch	7
Chiropotes satanas	7
Pithecia irrorata	7
Pithecia pithecia	8
Callicebus torquatus	12

Species	Incidence
Pithecidae	
Pithecia monachus	15
Callicebus cupreus	18
Cebidae	
Callithrix flaviceps	1
Callithrix geoffroyi	1
Callithrix penicillata	1
Cebus libidinosus	1
Saguinus inustus	1
Saguinus melanoleucus	1
Saimiri oerstedii	1
Callithrix aurita	2
Saguinus geoffroyi	2
Saguinus imperator	2
Saguinus nigricollis	2
Saguinus pileatus	2
Saguinus tripartitus	2
Callithrix argentata	3
Saguinus labiatus	3
Saimiri ustus	3
Cebus nigritus	4
Callithrix melanura	6
Saguinus midas	6
Saguinus mystax	6
Cebus capucinus	7
Cebus olivaceus	8
Saimiri boliviensis	9
Callithrix pygmaea	12
Saguinus fuscicollis	18
Cebus albifrons	28
Saimiri sciureus	30
Cebus apella	49

Table B6. Results of variation partitioning analysis of neotropical primate phylogenetic community structure for each metric independently into unique (a-c) and shared fractions (d-g) explained by environmental (ENV), historical (HIS) and spatial (SPA) processes. Adjusted R^2 values in bold are statistically greater than expected based on permutation tests.

Names/fractions		PD	ATA	MPD	MNTD
Environment (ENV)	**Adj.R^2**	**0.354**	**0.389**	0.014	**0.216**
	p-value	***0.000***	***0.000***	*0.144*	***0.000***
Historical (HIS)	**Adj.R^2**	**0.466**	**0.539**	**0.190**	**0.377**
	p-value	***0.000***	***0.000***	***0.001***	***0.000***
Spatial (SPA)	**Adj.R^2**	**0.563**	**0.509**	**0.512**	**0.489**
	p-value	***0.000***	***0.000***	***0.000***	***0.000***
ENV∩HIS	**Adj.R^2**	**0.536**	**0.599**	**0.188**	**0.422**
	p-value	***0.000***	***0.000***	***0.001***	***0.000***
ENV∩SPA	**Adj.R^2**	**0.564**	**0.599**	**0.507**	**0.507**
	p-value	***0.000***	***0.000***	***0.000***	***0.000***
HIS∩SPA	**Adj.R^2**	**0.614**	**0.672**	**0.574**	**0.528**
	p-value	***0.000***	***0.000***	***0.000***	***0.000***
ENV∩HIS∩SPA	**Adj.R^2**	**0.617**	**0.714**	**0.568**	**0.548**
	p-value	***0.000***	***0.000***	***0.000***	***0.000***
Independent fractions					
a- ENV|(HIS∪SPA)	**Adj.R^2**	0.003	**0.042**	-0.007	0.020
	p-value	*0.380*	***0.024***	*0.421*	*0.252*
b - HIS|(ENV∪SPA)	**Adj.R^2**	0.053	**0.115**	**0.061**	0.040
	p-value	*0.173*	***0.044***	***0.089***	*0.237*
c - SPA|(ENV∪HIS)	**Adj.R^2**	**0.081**	**0.115**	**0.379**	**0.126**
	p-value	***0.042***	***0.068***	***0.000***	***0.031***
Shared fractions					
d - (ENV∩HIS)|SPA	**Adj.R^2**	-0.002	**0.048**	0.002	-0.002
	p-value	*0.548*	***0.062***	*0.425*	*0.574*
e - (HIS∩SPA)|ENV	**Adj.R^2**	**0.129**	**0.095**	**0.114**	**0.165**
	p-value	***0.001***	***0.015***	***0.000***	***0.000***
f - (ENV∩SPA)|HI	**Adj.R^2**	**0.067**	0.018	0.005	0.025
	p-value	***0.011***	*0.325*	*0.195*	*0.140*
g - ENV∩HIS∩SPA	**Adj.R^2**	**0.286**	**0.281**	**0.013**	**0.173**
	p-value	***0.000***	***0.000***	***0.050***	***0.000***
Unexplained variation					
h - 1–(ENV∩HIS∩SPA)	**Adj.R^2**	0.383	0.286	0.432	0.452
	p-value	*1.000*	*1.000*	*1.000*	*1.000*

Note: (∩ intersection; ∪ union; | after controlling for).

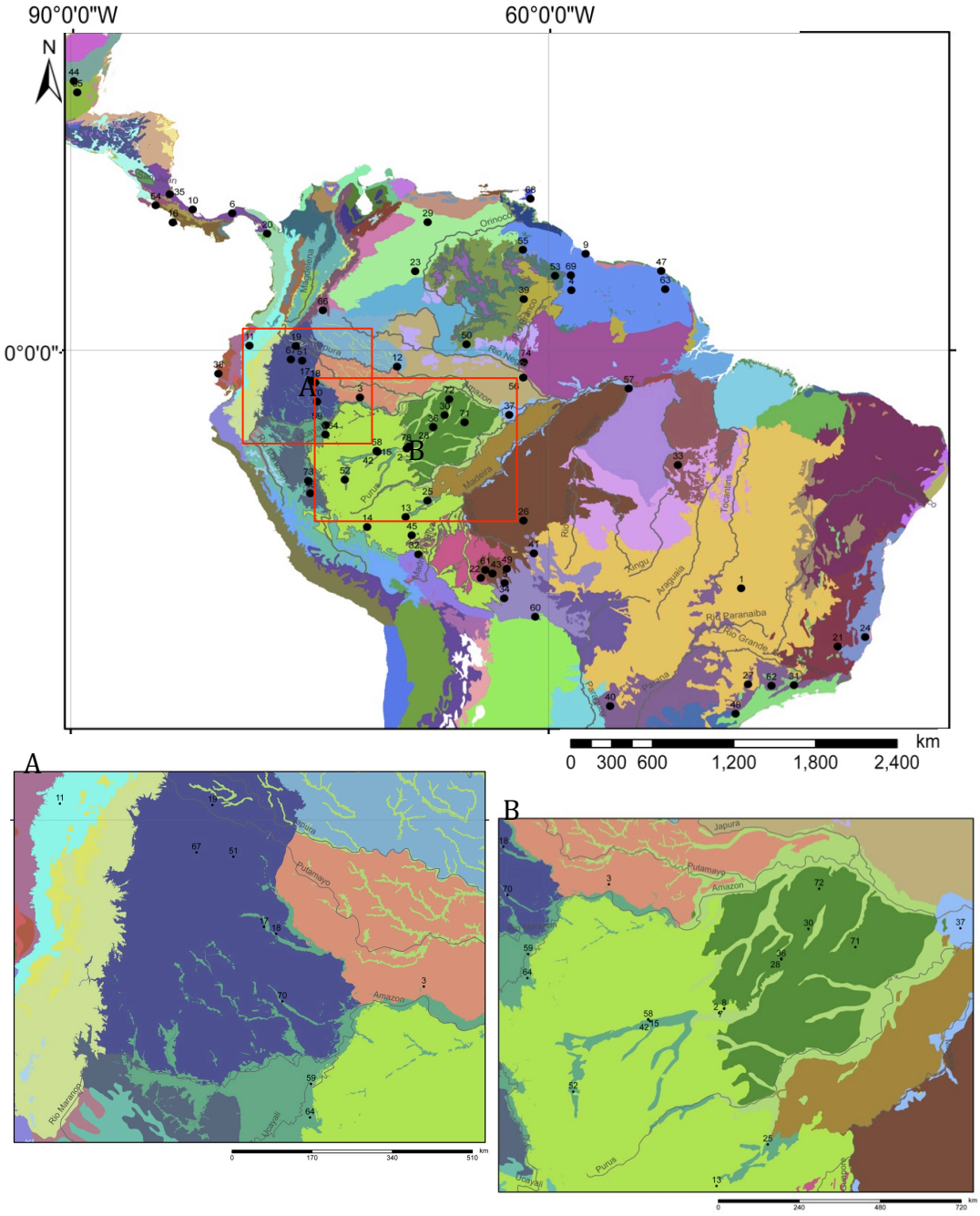

Figure B1. Communities included in the study overlaid on a map of terrestrial ecorregions by the World Wildlife Fund (Olson *et al*., 2001). Numbers correspond to those in Table B1.

(**Figure B1.** continued – Legend)

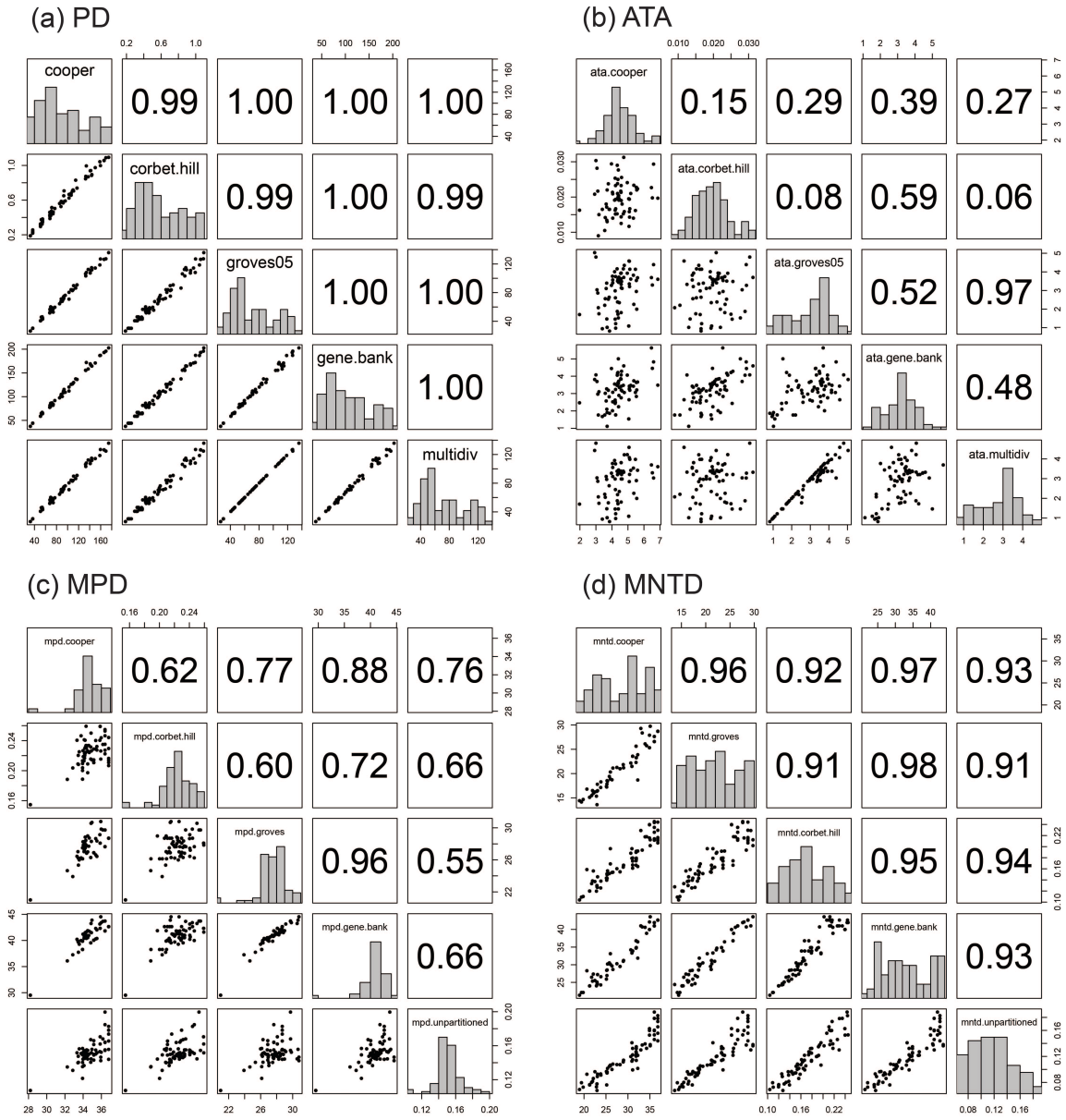

Figure B2. Scatterplot matrices showing Pearson correlation coefficients for each phylogenetic metric used **(a)** Phylogenetic diversity - PD; **(b)** Average Taxon Age - ATA; **(c)** Mean pairwise distance - MPD; **(d)** Mean nearest taxon distance - MNTD) – using multiple phylogenies: Cooper *et al*., 2008 with taxonomy from Wilson & Reeder (1993) – 52 sp.; Arnold *et al*., 2010 with taxonomy from Corbet & Hill (1992) – 36 sp.; Fabre *et al*., 2009 with taxonomy from Groves (2005) – 60 sp. (**used in analyses); Arnold *et al*., 2010 with taxonomy from Gene Bank – 44 sp.; and Fabre *et al*., 2009 with taxonomy from Groves (2005) using MULTIDIVTIME molecular dating estimates – 48 sp.

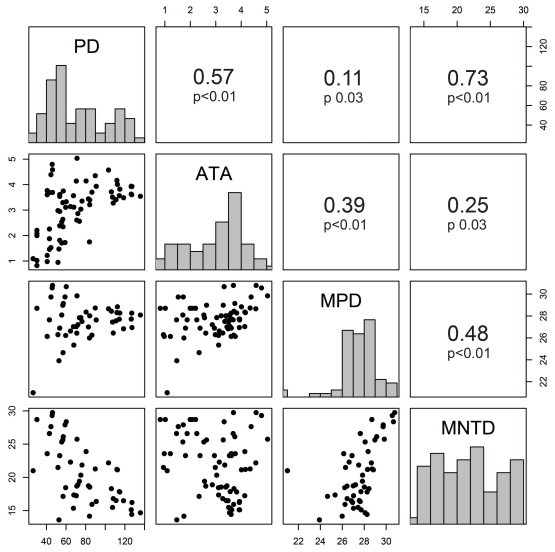

Figure B3. Scatterplot matrix showing Pearson correlation coefficients between phylogenetic diversity metrics used for analyses (Phylogenetic diversity - PD; Average Taxon Age - ATA; Mean pairwise distance - MPD; Mean nearest taxon distance – MNTD).

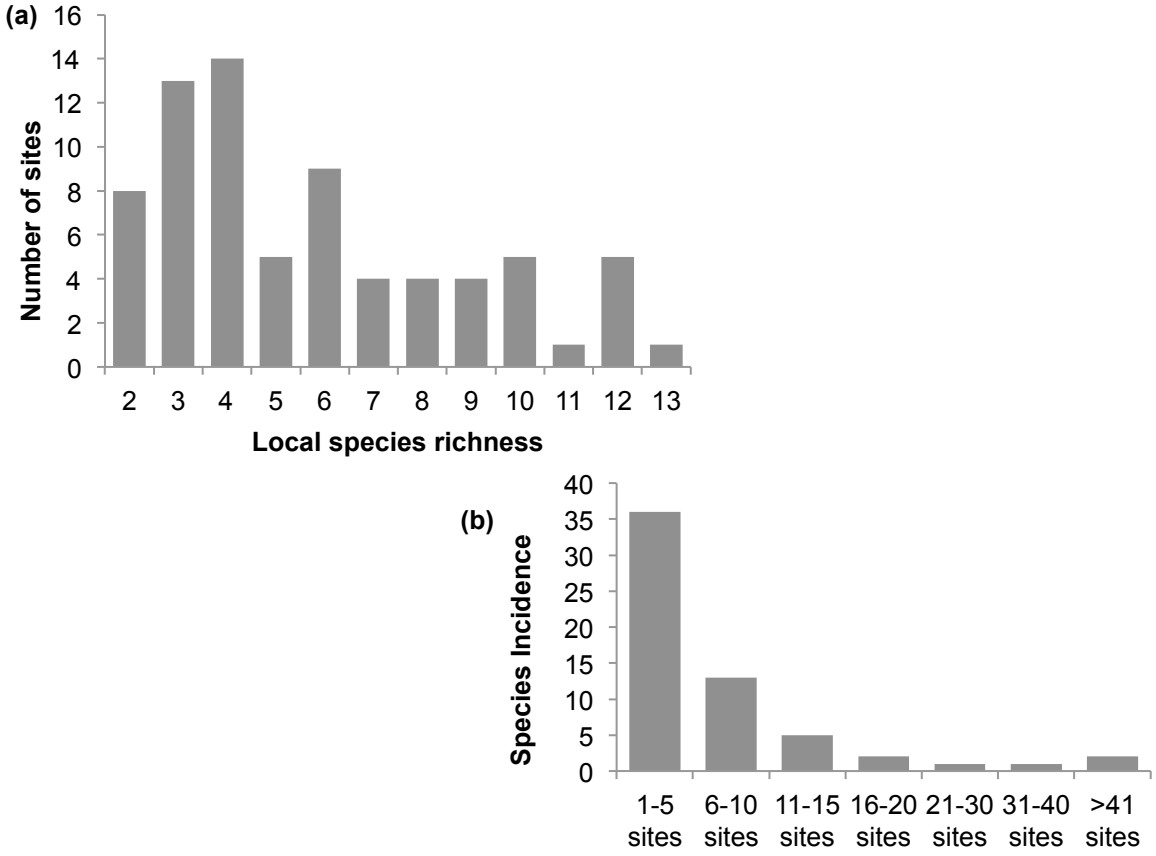

Figure B4. (a) Frequency distribution of sites in terms of primate species richness; (b) Primate species incidence by number of sites.

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APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table C. Habitat variables (and respective categories) recorded in each 10 × 10 m availability and occupancy plot.

Variables measured	Class	Categories
Forest type	Electivity[a]	Primary / Primary-gap / Secondary / Secondary-gap
Topography	Electivity[a]	Base / Valley / Hillside / Hilltop
Soil type	Electivity[a]	Firm / Floodplain
Water body close by (20m)	Binary[b]	Yes/ No
Canopy coverage	Percentage[c]	Percent coverage (densitometer)
Canopy connectivity	Categorical[d]	1(low) - 4 (high)
Phenology (PC-74.3%)	Proportion[e]	Percentage of trees with: new leaves, flowers, unripe fruits, ripe fruits
# dead trees	Count[f]	
Presence of stands of *Guadua bamboo*	Binary[b]	Yes/ No
Tree density (PC-70%)	Proportion[e]	Number of trees
Height (PC-84%)	Proportion[e]	Height of trees (m)
DBH (PC-89%)	Proportion[e]	DBH (m)
Crown diameter (PC-73%)	Proportion[e]	Crown diameter (m)
Epiphyte cover (PC-79%)	Proportion[e]	Percentage coverage of epiphytes in branches and main stem

[a]*Electivity: resource selection variables, where use by species may be higher/lower than expected based on its availability.*
[b]*Binary: Variable representing presence/absence of a particular kind of feature in a species plot.*
[c]*Percentage: Numerical response variable, bounded between 0-100.*
[d]*Categorical: Categories of a feature, which are assumed to be equally available to species to all species.*
[e]*Proportion: Numerical response variable, bounded between 0-1*
[f]*Count: Numerical response variable, not treated as a continuous variable, and bounded only at its lower extreme (0).*

APPENDIX D. PERMISSIONS TO REPRINT PUBLISHED CHAPTER

Permission for chapter 3

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VITA

Maria Mercedes Gavilanez was born in 1982 in Quito, Ecuador to her loving parents, Patricio Gavilanez and Sonia Endara. She showed a passion for animals since an early age, collecting every little critter that happened to pass along their backyard, or up in the hills at her grandparents' house on the coast where she spent her long summers with her two brothers. From age 12 to 17 she was an active member of the scouts movement, where she got to really experience the outdoors, fueling her passion for nature. In high school, she specialized in chemistry and biology, with the interest of becoming a veterinary doctor. Somewhere during her high school years she realized that being a biologist was a lot more interesting, because you get to work with the "weird" animals. She graduated from high school and started college at Pontificia Universidad Católica del Ecuador in the Biology program. She was always interested in studying mammals, particularly primate behavioral ecology. In 2003, she joined the Mammalogy section of the Zoology museum at the university, where she worked as a curatorial assistant for two years. During this time she was involved in projects involving ecology of bats and rodents, but her primate interest never diminished. She attended a field course on primate behavior, ecology, and conservation in Argentina, during her final year of college. This experience not only confirmed her interest in primates, but also stimulated a strong research interest in their ecology. Maria Mercedes graduated from college and obtained her *Licenciatura* degree in January 2007, after completing a research thesis investigating density, activity patterns, and habitat preferences of three primate species in Los Cedros, a cloud forest located in northwestern Ecuador and part of the Chocó-Darién biodiversity hotspot. A week after defending her *Licenciatura* thesis, she moved to the United States to join the Department of Biological Sciences at Louisiana State University to begin a doctoral program in biology under the supervision of Dr. Richard Stevens. Her dissertation research involved combining phylogenetic and taxonomic information to better understand neotropical primate species distribution and community structure at multiple spatial scales. She is also interested in conservation biology of tropical ecosystems and in the future hopes to contribute to bridging the gap between science and environmental policy implementation in Ecuador.